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ECOLOGY OF *MYSIS RELICTA* IN TWIN LAKES, COLORADO

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16. ABSTRACT

The Mt. Elbert Pumped-Storage Powerplant at Twin Lakes, Colo., is a major feature of the Bureau's Fryingpan-Arkansas Project. Twin Lakes are oligotrophic lakes of glacial origin located in the montane zone of the Rocky Mountains. The lake trout fishery at Twin Lakes is one of the best in Colorado. The major source of food for the lake trout in recent years has been *Mysis relicta* Loven, introduced to Twin Lakes in 1957. Vertical migrations of this freshwater mysid were studied using three ring nets and a benthic sled towed simultaneously on a single cable. It was learned that migrations vary in timing and magnitude and that juveniles migrate more extensively than adults. Horizontal distribution and movements were determined from trawls taken at 17 stations monthly for 2 years. The frequency distribution of *Mysis* per square metre was fitted to the negative binomial frequency distribution, indicating a highly clumped distribution for benthic *Mysis*. Deep and shallow water sample comparisons showed *Mysis* prefer deeper, colder water in the summer, migrating into shallow water in the fall. Studies of the effects on *Mysis* mortality of turbulence and turbidity created by plant operation revealed that 8 hours of turbulence daily greatly increased mortalities due to exhaustion and mechanical abrasion. Whether such attrition will adversely affect the population is not known.(64 ref)

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ECOLOGY OF *MYSIS RELICTA* IN TWIN LAKES, COLORADO

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by

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December 1976

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UNITED STATES DEPARTMENT OF THE INTERIOR * BUREAU OF RECLAMATION

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FOREWORD

This is one of a series of reports resulting from research being done on the environmental impacts of pumped-storage operation at Twin Lakes, Colo. This report is based on a master's thesis completed by Ronald E. Gregg in the Department of Fishery and Wildlife Biology at Colorado State University in April 1976. The work was cosponsored by the Colorado Division of Wildlife and the Bureau of Reclamation.

The Twin Lakes studies have been divided into pre- and post-operation phases. This report provides essential background information on one of the more important components of the Twin Lakes ecosystem. *Mysis* shrimp are responsible for the very good lake trout fishery that exists at Twin Lakes. Any condition affecting the shrimp population, then, would also affect the fishery. Following the commencement of pumped-storage powerplant operation, most of these studies will be repeated. Thus, any changes in the population structure of shrimp at Twin Lakes will be documented. Results from studies on the physical and chemical factors, as well as the other biological components, will provide the reasons for the changes that might occur.

This report will be useful to those concerned with the environmental aspects of Twin Lakes. For example, the data can be used to compute the times when shrimp are least likely to be damaged by pumping, thus permitting operating schedules to be adjusted so that shrimp are not unnecessarily affected adversely by pumping. In addition, results of laboratory studies on the effects of turbidity and turbulence on shrimp are presented to give some insight into what might happen at Twin Lakes when the powerplant is operational. This report will also be of interest and use to anyone concerned with the impacts of pumped-storage operation on aquatic environments in general, especially those containing large plankters similar to *Mysis* shrimp. Finally, the information presented will be of use to those interested in freshwater shrimp, including fish and game agencies that are considering stocking cold-water lakes with shrimp with the objective of improving their fisheries. Twin Lakes, an example of a very successful plant, is now the source of supply for numerous transplants each year to lakes not only in Colorado, but also in other Western States.

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INTRODUCTION

The national demand for energy has increased the necessity for facilities that can generate and store electric power. A progressive approach to this problem is the concept of pumped-storage hydroelectric powerplants. Pumped storage is an economical and technically feasible means of generating low-cost, dependable peaking power, providing reserve generating capacity, and storing large quantities of energy for use on demand. This type of powerplant must be located adjacent to a body of water where large amounts of water can be pumped to and from the water system.

Since the environmental effects of pumped-storage powerplants are virtually unknown, the potential effect of this pumping activity on a body of water as a recreational area, as a fishery, and as an aquatic ecosystem must be determined and recognized if this type of powerplant is to be incorporated into power systems in an environmentally sound manner.

Twin Lakes, in the Rocky Mountains near Leadville, Colo., is the site of the Bureau of Reclamation's Mt. Elbert Pumped-Storage Powerplant, which was partially constructed at the writing of this thesis, April 1976, and is scheduled to begin initial operation in October 1977.

Twin Lakes, Colo., is a recreational area noted for its scenic beauty and as one of the best fisheries in the State for the lake trout, *Salvelinus namaycush*. Twin Lakes is also the site of a very successful introduction of the freshwater opossum shrimp, *Mysis relicta* Loven, as a forage species. A thriving population of this exotic shrimp has become a most important part of the trophic structure of the lakes. The population of *Mysis* in Twin Lakes is unique to the waters of Colorado. Of the many attempts at introducing *Mysis* into lakes in the Western United States, the introduction at Twin Lakes ranks as one of the most successful. *Mysis* are a major food source for the lake trout in Twin Lakes and are currently responsible for supporting a majority of the fishery in the lakes. If the operation of the powerplant should be detrimental to the *Mysis*, a unique and valuable fishery could be altered.

The purpose of this study was to determine the ecology of *Mysis relicta* in Twin Lakes and its relation to the construction and operation of the Mt. Elbert Pumped-Storage Powerplant.

This study was divided into four parts. In the first section a method for taking adequate samples of *Mysis* was examined and the diel vertical migrations that are characteristic of this species were studied. This vertical migration behavior is important to the trophic structure of the lake. Vertical migration during hours when water is being pumped from the lakes greatly increases the chance that *Mysis* will be entrained in the pump turbines. Snyder[1][1] estimated that 5.1 fish eggs per cubic dekametre (dam^3) and 43.8 young fish per cubic dekametre were pumped through the Muddy Run Pumped-Storage Plant from Conowingo Reservoir, Pa. *Mysis relicta* were found in the discharge from Ludington Pumped-Storage Plant on Lake Michigan.[2]

The second aspect of this study was to determine a detailed life history for Twin Lakes *Mysis*, including breeding period, time of recruitment, seasonal patterns of the life cycle, growth, and longevity.

In the third section, the distribution pattern of benthic-dwelling *Mysis* was examined and an attempt was made to elucidate the cause of spatial and temporal variation in mean areal densities. Environmental factors affecting distribution were also considered.

In the final section, the specific details of the design and operation of the Mt. Elbert Powerplant and tailrace channel were considered in conjunction with a series of laboratory experiments directed toward estimating possible effects of the powerplant on the *Mysis* population. In the conclusion, all aspects of this study were drawn together in predicting the possible impacts of the powerplant on the *Mysis* population.

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[1] Numbers in brackets refer to items listed in the bibliography.
[2] Charles Liston, Michigan State University, personal communication.

The Fryingpan-Arkansas Project

Twin Lakes and the Mt. Elbert Pumped-Storage Powerplant are essential features of the Bureau of Reclamation's Fryingpan-Arkansas Project. This is a multipurpose project with objectives including irrigation development, hydroelectric power generation, domestic and industrial water supply, water quality control, and the development of recreation while providing for preservation and propagation of fish and wildlife. The project was authorized in the U.S. Congress by Public Law 87-590 dated August 16, 1962.

The project plan includes works for diverting water to water-short areas on the eastern side of the Colorado Rocky Mountains. On the western slope of the mountains, collection facilities were constructed on the headwaters of the Roaring Fork and Fryingpan Rivers. Water impounded by these facilities is transported beneath the Continental Divide via the Boustead Tunnel to Turquoise Lake on the eastern slope. The water is stored there and is released as needed into the Mt. Elbert Conduit, which carries it down to the Mt. Elbert Forebay overlooking Twin Lakes. Water can be held in the forebay or released through penstocks to pass through the Mt. Elbert Pumped-Storage Powerplant and then into Lower Twin Lake (fig. 1).

The pumped-storage powerplant has both generating and pumping cycles. During periods of peak power demand, water will be released from the forebay to operate turbine-driven generators. During periods of minimum power consumption, water will be pumped to the Mt. Elbert Forebay from Lower Twin Lake. Power can thus be stored in the potential energy of water at the upper end of the penstocks. Approximately 3 kilowatts are consumed in the pumping cycle for every 2 kilowatts produced during the power generating cycle. Despite the apparent net loss of energy, the concept is attractive because (1) of the economic advantage of buying low-priced power during periods of low demand and selling the power at a higher rate during peak demand periods, (2) pumped storage is a much more efficient source of peaking power than is a fossil fuel powerplant (70 vs. 40 percent), and (3) pumped-storage power is available almost instantly, whereas thermal plants require half an hour to be brought online.

Historical Importance of "Mysis relicta"

Mysis relicta Loven is commonly called the opossum shrimp. The taxonomic classification is noted below.

Class Crustacea
Subclass Malacostraca
Division Peracarida
Order Mysidacea
  Suborder Mysida
    Family Mysidae Dana
    Subfamily Mysinae
      Tribe Mysini
        Genus *Mysis* Latreilla
        Mysis relicta Loven

Mysis relicta is a fresh- and brackish-water form considered to be a glacial relict. This species is very similar to the marine species *Mysis oculata* [3]. During the glacial periods, mysids were pushed ahead of the ice sheets into lakes along the ice margins. *Mysis relicta* is derived from these surviving glacial relicts [4]. The occurrence of *Mysis relicta* in brackish ponds on the arctic coast [5] and in many northern glacial lakes support this theory.

The distribution of *Mysis relicta* follows a circumpolar arctic pattern, following the southern edge of Pleistocene glaciation [4]. On the North American continent, they are found in cold temperate and arctic lakes across Canada and in the northeastern states east of the Great Plains.

The economic value of mysids in fisheries is the basis for most present interests. The production of sport fish in a lake can be increased by the introduction of *Mysis* as a fish food source. As early as 1939, W. A. Clemens suggested introducing *Mysis* into a British Columbia lake to enhance the fishery [6]. Transplants were first made in 1949 into Kootenay Lake in British Columbia. In Sweden, Furst [7] reported that mysids have been stocked since 1954 in a variety of lakes to replenish the food supply of trout and char that had been reduced by water fluctuations caused by a hydroelectric facility. Beginning about 1963, state fish and game management agencies in the Western United States and Canada became actively interested in the potential of *Mysis* as a food source for cold water fishes.

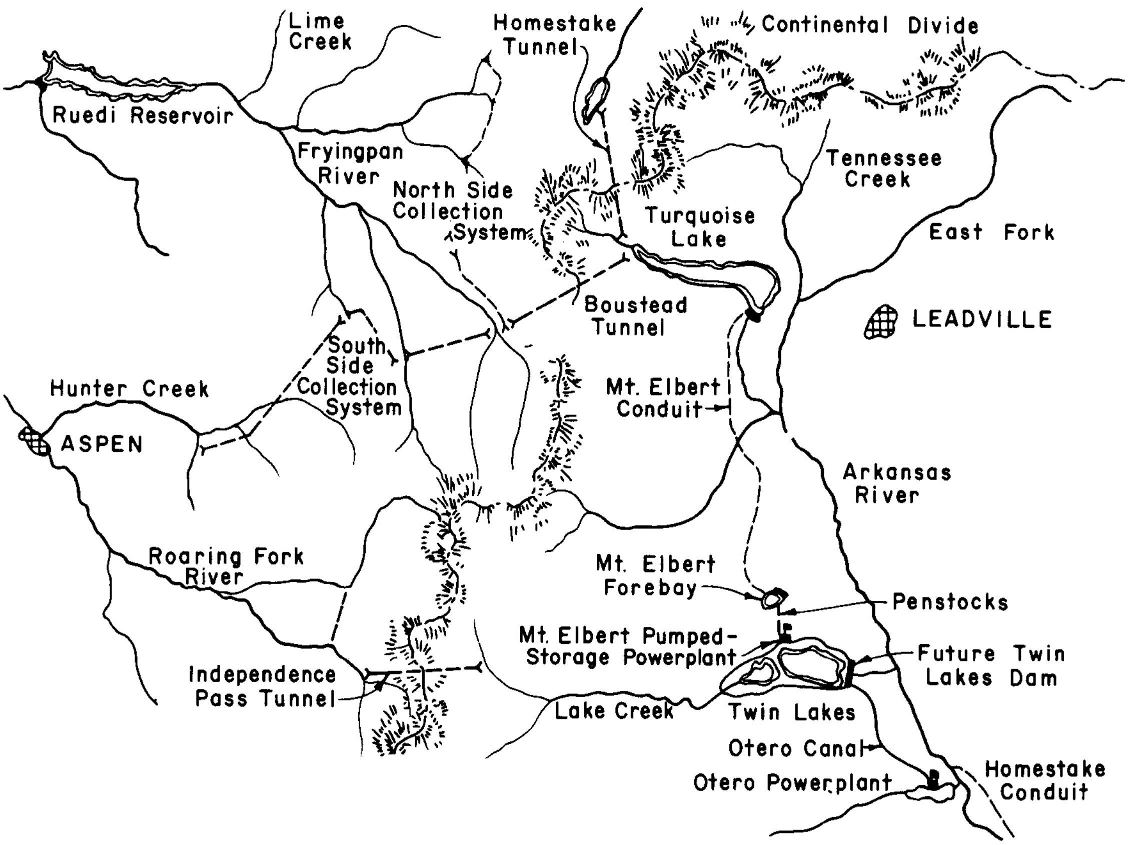

Figure 1.–Map of the Fryingpan-Arkansas Project showing the major features of the western and upper eastern slope areas (adapted from [2]).

California, Nevada, Washington, Montana, other Western States, and British Columbia have developed stocking methods and programs to establish *Mysis* in cold water fisheries. Waterton Lake, Alberta, has been the source of mysids for several transplants.

Only partial success has resulted from a variety of transplant attempts. Lake Kootenay, British Columbia, was the site of the earliest successful transplantation. The delay factor in establishing a population was about 10 years [8]. Lake Tahoe in California and Nevada has developed a population large enough to supply mysids for further introductions. Trinity Lake in California also has a reproducing population. Other successful transplantations recorded at this time are Grindstone Lake, Minn., and Priest Lake, Idaho [8].

Mysis relicta is a large zooplankter which inhabits a niche that is unexploited in many cold, deep, oligotrophic lakes. Introduction of *Mysis* can create a new food source for fish from a region that, in many lakes, is usually unproductive. In developing a fishery, the introduction of *Mysis* has the effect of bringing nutrients back into the system that may have otherwise been lost. During daylight, mysids are mainly benthic dwellers. They feed on organic materials found in the surface layer of bottom mud. Protozoans, mud-living diatoms, algae, and detrital material sinking into the bottom from the epilimnion are utilized. In this way, *Mysis* make available to fish energy that may have otherwise been lost. Benthic and deep water fishes are the major predators on mysids, but their diel vertical migrations into upper strata make them available to epilimnetic fishes during hours of darkness.

The utilization of *Mysis* by fish and their corresponding increase in growth has been well documented. Several studies have shown the value of native populations of *Mysis* in the diet of trout [9, 10]. *Mysis relicta* were the major food of immature lake trout in Green Lake, Wis.[11] In this lake the growth rate of lake trout increased three times when *Mysis* were abundant. Rawson [12] showed that lake trout from 180 to 400 mm in length utilized *Mysis* for 17 percent of their total food volume intake. Mysids are most valuable to juvenile and intermediate-sized fish that are too small to feed on other fishes. Forage fishes such as American smelt, alewives, ciscoes, sculpins, bloaters, whitefish, and sticklebacks have been shown to feed on *Mysis* [8]. Since many of these fish are eaten by larger lake trout, mysids can contribute both directly and indirectly to the production of sport fish. Larkin [9] observed this in Great Slave Lake. In Lake Tahoe, Calif., mysids were introduced in 1965. Stomach analysis in 1972 showed that 60 percent of mackinaw between 380 and 500 mm in length contained *Mysis* [13].

"Mysis relicta" in Colorado

Twin Lakes, Colo., was stocked with *Mysis relicta* on October 3, 1957. It is interesting to note that the introduction consisted of a single thermos containing the shrimp.[3] The introductory plant of *Mysis*, which came from Clearwater Lake, Minn., and contained between 600 and 1,000 mysids, were released in a single bay in the lower lake. The population has grown extensively and large numbers are ubiquitous in both the upper and lower lakes. Predation on *Mysis* has become quite extensive. Lake trout, especially juveniles, feed heavily on them. Eighty-seven percent of lake trout examined in 1974-75 contained some *Mysis* and at times the trout feed almost exclusively on *Mysis* [63].

The Twin Lakes fishery, as it exists at this time, is rated as an outstanding lake trout fishery. The fishing at the lake is a major attraction, bringing vacationers and fishermen to the area. The fishery is estimated to be worth $500,000 per year [14].

Twin Lakes is the sole source of *Mysis* used in stocking programs at many Colorado lakes. The extremely abundant shrimp are easily collected. Twin Lakes mysids have also been used by other states for transplants. Fifty-seven lakes in Colorado, Wyoming, Utah, and North and South Dakota have been stocked with *Mysis* from Twin Lakes. Methods include aerial stocking in high-country lakes.

Description of the Twin Lakes System

Twin Lakes was originally two separate lakes connected by Lake Creek. Early in the century, a dam was constructed at the outlet of the lower lake. Later, the dam was modified and the stream channel between the lakes enlarged, so that now the two lakes function as one reservoir, storing irrigation water brought by tunnel under the Continental Divide [14].

Twin Lakes lies a short distance below the mouth of Lake Creek Canyon, occupying a basin on the eastern side of the Sawatch Mountain Range. On the northwest, Colorado's highest peak, Mt. Elbert, rises to an elevation of 4395.5 metres. The surrounding peaks are markedly glaciated, and glacial till is the characteristic deposit around the basin of the lakes. Thus, the lakes are entirely surrounded by morainal detritus. The lakes were formed when a glacier moved down from the western peaks, scoured out the basins and then receded, leaving the morainal ridges visible today curving around the lower lake from the foot of Mt. Elbert. The low ridge separating the two lakes and running parallel to the other ridge is also a morainal deposit. These moraines blocked the flow of Lake Creek, and subsequent filling of the basins created Twin Lakes [14].

The maximum water surface elevation of Twin Lakes is 2802 metres. Maximum depths are about 28 metres for the upper lake and 27 metres for the lower lake. Lake surface areas corresponding to these maximum depths are approximately 263 hectares for the upper lake and 737 hectares for the lower.

The bottom of Twin Lakes is composed mainly of glacial sediments. Samples taken from various stations within the lakes are mineralogically similar. Some parts of the lake bottoms are covered with gravel and and boulders of various sizes, but the primary cover consists of clay-sized particles of rock flour. The bottom of the connecting channel is mostly sand. Studies indicate that the bottom of the lower lake is covered with an unconsolidated layer of sediment resulting from glacial action and stream deposition [15].

[3] Larry Finnel, Colorado Division of Wildlife, personal communication.

Observations of Bottom Sediments and Aquatic Vegetation from Scuba Dives

Glacial flour sediments were easily put in suspension by diving activities, and the resulting turbidity was evident for 2 days following dives. A diver would sink as much as 300 mm when standing on this type of bottom [16]. Sediments of this nature covered the bottom of both lakes at depths from 4.6 to 23 metres.

Observations made during scuba dives at Twin Lakes have yielded valuable information on the makeup of the bottom, the vegetation, and general estimates on mysid behavior and abundance. Both lakes have a similar makeup of bottom sediments.

The lakes have a gently sloping zone from shore to a depth of about 3 metres which is made up of large rocks and is lacking in vegetation. The slope then abruptly increases to approximately 45°. The rocky bench is the remnant of the old shoreline before the dam was constructed. Vegetation begins in the 45°-slope zone and, depending on the steepness of descent, is found in strips of varying width. Pondweed, *Potamogeton amplifolius*, grows quickly during summer months. It was recorded to increase in size from 1 to 4 metres from June to August. This occurs for depths from 3 to 10 metres. Following these strips, the stonewort, *Chara globularis*, become dominant. *Nitella opaca* is also found in these areas. As depth increases, rooted vegetation stops completely. Glacial flour covers the rocks at depths from 12 to 21 metres. There is a distinct interface in both lakes where the glacial flour sediments completely cover the rocks. The depths of both lakes are dominated by this soft, unconsolidated material. The eastern end of the lower lake is the major exception to this pattern. It is gently sloping and requires a hundred metres or so to reach a depth of 10 metres. This area has very abundant vegetation, dominated by pondweed. By the end of summer, this aquatic plant reaches to the surface in some areas. It was noted that much of the vegetation was coated with layers of glacial flour sediment.

Twin Lakes Fishes

Twin Lakes supports a reproducing population of lake trout, *Salvelinus namaycush*, which is the major sport fish in the lake. Planted rainbow trout, *Salmo gairdneri*, constitute a put-and-take fishery. The white sucker, *Catostomus commersoni*, is the most common fish numerically. It is the only native fish species that still occurs in Twin Lakes. Other fishes found in Twin Lakes are brown trout, *Salmo trutta*, cutthroat trout, *Salmo clarki*, Kokanee salmon, *Oncorhynchus nerka*, and the longnose sucker, *Catostomus catostomus*.

Physical-Chemical Limnology

Data on physical and chemical properties of Twin Lakes have been gathered by Bureau researchers in conjunction with extensive limnological investigations since 1971 [4]. A review of these data is included because of the importance of physical and chemical properties to *Mysis relicta*. The exact nature of the water quality required by *Mysis* is unknown. *Mysis* seem to be very adaptable as evidenced by the study of Lasenby and Langford [17] who reported them in both an oligotrophic arctic lake and a eutrophic temperate lake. In opposition to this contention lies the failure of many attempts at stocking *Mysis* in lakes that seem to be very similar. In Colorado, a reservoir on the same drainage system as Twin Lakes, Turquoise Reservoir, has been stocked with *Mysis* and yet the mysids have failed to become established.

Twin Lakes are dimictic lakes. Temperature stratification begins in June and reaches a maximum in August. Bottom temperatures reach a maximum of slightly less than 7 °C and maximum surface temperature is 14 °C in July and August. Fall overturn comes in October and the lake is isothermal at 4 °C by November. Temperature profiles taken through the ice in the winter show an inverse stratification, with 4 °C at the bottom and 0 °C water on the surface. Temperature isotherms are nearly horizontal across the lower lake on most occasions. Tilted isotherms can be created by wind piling up surface waters at one shoreline [14].

Dissolved oxygen profiles show a direct dependence on temperature stratification and overturns. Dissolved oxygen is at 7 mg/l at all depths when the ice goes off the lake. Oxygen is depleted in deeper areas as summer progresses, reaching lows in August through September of 1.5 to 2.5 mg/l at depths below 21 metres. Fall overturn returns levels to 8 to 9 mg/l.

Light penetration was measured using a limnophotometer. Light extinction coefficients taken in March through the ice gave values of 0.33 m^{-1} in the center of the lower lake and 0.36 m^{-1} in the upper lake. The lake was less clear in the fall with 0.62 m^{-1} in the center of the lower lake.

Results of chemical analyses performed by Bureau personnel are contained in a 1973 progress report [14]. The water quality of Twin Lakes is very good. Conductivity values are low, ranging from 52 to 91 microsiemens at 25 °C. Dissolved solids range from 32 to 88 mg/*l*. The principal cation is calcium, which ranges from 8.8 to 12 mg/*l*, while the principal anion, bicarbonate, ranges from 20 to 30.5 mg/*l*. Sulfates were also important, ranging from 8 to 26 mg/*l*. Analyses for heavy metals gave the following values: copper, 0 to 0.95 mg/*l*; iron, 0 to 1.5 mg/*l*; zinc, 0 to 71 mg/*l*; and manganese, 0 to 0.8 mg/*l*.

SAMPLING "MYSIS" AND VERTICAL MIGRATIONS

Introduction

Vertical migrations of *Mysis relicta* in Twin Lakes were investigated for several reasons. Basic knowledge on mysid behavior as an exotic in an alpine lake is valuable. Introduction of *Mysis* into a lake can make a significant impact on the trophic structure of the ecosystem. The manner in which the system is affected is directly related to the extent of vertical migrations. By feeding on bottom detritus, mysids pick up nutrients and energy that have settled from the overlying water [18]. Daily vertical migrations return these nutrients to the water column where they can be utilized by fish. Vertical migrations also have the effect of bringing *Mysis* into contact with the existing pelagic population of zooplankters. Lasenby [19] found that the diet of mysids varied between lakes and with the time of sampling. At night, mysids which had migrated into upper waters fed on Cladocera, Rotifera, Protozoa, Chlorophyceae, Bacillariophyceae, assorted pennate and centric diatoms, and pollen grains. Mysids may deplete existing zooplankton populations by predation or by successful competition with the existing zooplankters. This is partially dependent on the numbers of mysids migrating and on the length of migrations.

Vertical migrations in Twin Lakes will take a portion of the mysid population directly past the entrance to the powerplant tailrace channel. If the plant is operating in the pumping mode during the migration, *Mysis* may be entrained in the flow to the pumps. Knowledge of the extent and timing of the vertical migrations is needed to predict the impact of powerplant operation on the mysids. Entrainment of a significant percentage of the nightly migrators could have an adverse effect on the total population.

Diel migrations in the water column have been found in organisms from fish to the smallest plankters. Migrations among planktonic crustacea have been well documented in both marine and lacustrine habitats. Aspects of these investigations include: timing of migrations; length of migrations; percentage of population involved; differential migrations of age, sex, or maturity classes; and causes behind the migrations. Cushing [20] presented a description of vertical migrations and a summary of hypotheses to explain the phenomena. He concluded that vertical migration in planktonic crustacea is mediated by the change in light penetration throughout the day.

Four main phases in the migrational pattern which are principally dependent on light density are identified. Evening ascent is triggered by decreasing light intensity. Midnight sinking is assumed to be due to a passive state in full darkness. A rise to the optimum light intensity for the population takes place at dawn, followed by a rapid descent to depths caused by increasing sunlight. Environmental factors such as temperature, dissolved oxygen, turbidity, and food availability may affect the patterns of migration.

Mysis relicta has been the subject of several vertical migration studies. Juday and Birge [21] reported finding *Mysis* in the surface waters of Wisconsin lakes during hours of darkness. Larkin [9] reported that mysids migrate actively in lakes in northern Canada. Recently, more detailed investigations have been made on *Mysis* migrations and it appears that vertical migrations are quite variable from one lake to the next. Holmquist [22] raised the question as to whether these movements are actually migrations or merely a random wandering and dispersal due to the absence of light and the widening of the tolerable world around them. Beeton [18], who made a comprehensive study of the vertical movements of *Mysis* in the Great Lakes, concluded that diurnal changes in the vertical distribution of *Mysis* are the result of regular vertical migrations. Opposite findings were reported by Lasenby [19] who found no vertical migrations by *Mysis* in oligotrophic Char Lake. Apparently vertical migrations can be modified by physical or biological conditions present in the lake.

Differential migrations of different size classes complicate the analysis of migration patterns. This also complicates the sampling of the population as discussed in the next section. Teraguchi [23] studied the timing, migratory patterns, and vertical distribution of different instars of both sexes of *Mysis*. Age groups of zooplankton have been shown to inhabit different depths in several studies [24, 25, 26]; differing sensitivities to environmental factors including light and temperature are possible reasons. The possibility of a social behavior for *Mysis* does exist. Clutter [27] found zonation patterns and aggregation into swarms and schools in marine mysids. Brownell [28] and Beeton [18] concluded that young *Mysis* migrate upward farther and sooner and descend later and not as far down as adults.

Teraguchi [23] stated that there is a general tendency for the onset of ascent to be progressively later with increase in age of the males and females and for the initiation of descent to be progressively earlier with increase in age of males and females, with age influencing migration more than sex. Differences in photosensitivity are determined by the age of the animal which in turn determines migration patterns. Teraguchi found this general tendency, but distinct patterns for sex and age groups were not consistent. Distinct social interactions such as swarming have not been reported.

Sampling Methods Review

Methods previously used for sampling *Mysis* are varied and were given careful consideration in planning this study. Knowledge of mysids' behavior and distribution patterns in nature is indispensable for precise sampling estimates. The previous discussion on mysid migrational patterns indicates that *Mysis relicta* can be both a plankter and a benthic animal. This initiates the question of sampling *Mysis* on the bottom versus in the water column.

Preliminary daytime tows in Twin Lakes taken with a 1-metre net of 700 nitex mesh occasionally took numbers of immature *Mysis* in the water column during the day. Beeton [18] reported that most *Mysis* are near the bottom during daylight. Reynolds and Degraeve [29] believed that benthic sampling during the daytime offered the best opportunity to obtain representative samples of the population. These authors noted a discrepancy in their sample catches, possibly due to a failure to look at distribution in the water column:

> Although young *Mysis* are commonly released from the brood pouch at a length corresponding to the 3-mm size groups [30], individuals of this size group were never abundant in the samples—including those collected in April and May, when spent females were prevalent. However, 4-mm juveniles were dominant in 7 of 10 monthly collections. Probably a selectivity factor operated to reduce the probability of capture of mysids from the time of their release until they reached a length of 4 mm. If so, the bias could have resulted from either behavioral characteristics (e.g., newly released young are off the bottom) or net selectivity [29, p. 126].

One report of a very large daytime aggregation of *Mysis relicta* in the water column off the bottom was given by Robertson, Powers, and Anderson [31]. Direct observations from a submarine at six stations in Lake Michigan found *Mysis* almost entirely on the bottom at five of six stations. At one station, between a depth of 172 and 187 metres (time was 11:30 e.s.t.), mysids were found to be very abundant off the bottom. This supports the contention that *Mysis* populations are not always entirely on the bottom. Robertson, et al [31] concluded that *Mysis* are entirely on the bottom in water less than 85 metres in depth, while in deeper areas they are more dispersed in the water column.

Consideration was given to the avoidance of towed nets by zooplankton when planning this study. Crustacean zooplankton are all capable of oriented movement out of the path of sampling devices. The copepod *Labidocera acutifrons* is capable of directed movement at a rate of 0.76 m/s (230 body lengths per second) over a distance of 150 mm [32]. Sampling efficiency is diminished when animals are capable of avoiding the net. Experiments have been done to describe filtration in nets so that designs to decrease directional sensory cues ahead of the net can be developed. Acceleration forces inside nets produce "forward acceleration fronts," where some accelerated water is pushed to all sides ahead of the net. Factors which determine this are: (1) mesh aperture size, (2) ratio of mesh aperture to mesh filament, (3) ratio of mesh aperture area to net mouth area, (4) water temperature, and (5) velocity of the tow [32]. Marine mysids show a definite avoidance reaction to a sampler that produces a forward acceleration front. Animals at the source of disturbance alert those at the periphery by means of a noticeable avoidance activity [33]. Sampling efficiency was therefore maximized by using a net constructed to minimize the "acceleration front" effect. The mesh aperture had to be sufficiently small to capture *Mysis* of 3-mm length, and net size was limited by the equipment available for practical handling and towing.

Brownell [28] noted that a Miller High Speed Sampler was very inefficient in catching *Mysis*. Beeton [18] and Teraguchi [23] used Clarke-Bumpus samplers to obtain quantitative estimates of *Mysis* numbers. Beeton noted that the stated number of mysids present at a given depth is an approximation, but that it has considerable quantitative value. Teraguchi determined that the number of mysids caught in a single haul at one depth was reasonably representative and not a chance occurrence. Three Clarke-Bumpus samplers spaced as close as possible collected triplicate samples from a single depth. "Usually two of the catches were similar. The one that departed from the other two was never from the middle sampler, but was from the top of bottom sampler. This consistency in variation suggested that deviation of one of the catches from the other two was not a sampling error, but a variation resulting from the actual micro distribution of the mysids" [23, p. 10].

Considering the avoidance ability of mysids, it appears unlikely that small-diameter samplers like the Clarke-Bumpus would sample *Mysis* with high efficiency. A larger diameter net equipped with a flowmeter would sample with greater efficiency and thus would give more precise estimates of numbers of *Mysis*.

A reasonable alternative would be to employ a total vertical haul with a large-diameter net. Lasenby [19], Carpenter, Anderson, and Peck [34] and Foulds [35] have used this method. This would adequately sample the water column, but would fail to effectively capture mysids on the bottom.

In this study, the purpose of capturing mysids was to obtain a quantitative estimate of population density whether it was at the bottom or at various levels in the water column. In obtaining samples for size frequency analysis, it was essential to have all members of the population equally represented in the samples. This would entail capturing representatives of all animals on the bottom as well as those in the water column simultaneously.

Methods and Materials

Samples were taken simultaneously near the surface, at two intermediate depths, and at the bottom. Three nets and a benthic trawl attached to a single cable were used for each haul. This method is similar to that used by Herman [36] in a study of the vertical migration of a marine mysid *Neomysis americana*. It has the advantage of examining the distribution at three depths at a single instant, and at the same time obtaining information on the benthic population.

Nets were constructed of 0.706-mm nylon mesh. The nets tapered from 500-mm diameter to the cod end of 125-mm diameter in a distance of 1500 mm. Plastic cylinders with a screwcap were fitted with 0.706-mm fiberglass mesh to serve as plankton buckets. These were much easier to handle in freezing weather than conventional metal buckets. A benthic sled was constructed of aluminum tubing and the net was sewn to a rectangular aluminum frame. A rounded aluminum skid was attached across the front of the trawl to prevent it from digging into the soft sediments. A strip of tough canvas was attached from the trawl frame backwards to prevent the netting from snagging or tearing on debris. Flowmeters were suspended in the mouth of the nets using elastic bands. Pigmy flowmeters from Kahl Scientific Co. were used. Calibration for the flowmeters is given in table A-1 in the appendix. The sampling boat was equipped with a winch, metering wheel, and inclinometer. The depth at which each net would sample could be determined from the cable angle and the length of cable released. A preliminary haul would determine the approximate cable angle for a measured boat speed. Using this angle and the depth indicated by fathometer, the nets could then be attached so that the trawl was on the bottom, the first net was at two-thirds of total depth, the second net was at one-third total depth, and the third net was slightly beneath the surface.

The benthic sled was lowered with the boat stationary. At the first net attachment point, the boat was slowly moved forward while the remaining nets were attached. The boat then proceeded at a measured trawling speed for 10 minutes. At the end of this period, the boat was brought to a complete stop and the nets were raised vertically. A negligible amount of quantitative accuracy is sacrificed using this technique. At the end of each haul, data for the speed of the boat, length of haul, depth for each net, volume of water sampled, and notes on weather conditions were recorded. Samples were taken before sunset, after sunset, every 2 to 3 hours during the night, before sunrise, and after sunrise. These samples were taken once a month during ice-free periods.

Samples were taken in the northwest corner of Lower Twin Lake. This location, known as pump plant bay, was chosen because of its proximity to the construction site of the hydroelectric facility. It is necessary to restrict sampling to a single area to eliminate discontinuities in population structure and movement due to changes in substrate, water quality, or depth. Pump plant bay is ideal for sampling because it has a depth variation of only 1.5 metres, a flat bottom, and a consistent glacial flour substrate. Debris and plant material were never encountered in samples from this area. Bottom debris can greatly complicate operation of the benthic sled.

Twin Lakes is ice covered for about 6 months of each year, from early December to sometime in late April to late May; therefore, it was necessary to develop a sampling method for taking *Mysis* through the ice. Early in December when the ice was 100 mm thick, a transect was laid out in pump plant bay. A rope 122 metres long was put underneath the ice by means of an ice jig. This device "swims" forward about a metre each time it is pulled backwards with an attached rope. When the ice is thin the device can be located easily. The rope was weighted to sag beneath the ice and the ends were allowed to freeze in. Care was taken to assure that the rope sagged enough and did not freeze into the ice entirely as the ice became thicker.

Each month, when weather conditions permitted, samples were taken through the ice. The benthic sled was attached to the bottom of the cable and lowered. The nets were attached to sample two-thirds depth, one-third depth, and the surface. The top end of the cable was attached to a float which connected to the rope under the ice. The float served to keep the top nets just below the surface and the middle nets evenly spaced. The nets were pulled between the ends of the transect by walking or by snowmobile. A trailer line allowed this procedure to be repeated from either end of the transect. Samples were thus collected at the surface, two depths, and the bottom simultaneously, as was accomplished during open water periods.

Monthly samples taken on one night during each of the 6 open-water months consisted of a maximum of eight hauls. Each haul contained four samples, one from each of the corresponding sampling depths. The entire sample from each net was preserved independently in 10 percent formalin and returned to the laboratory for analysis.

Winter samples were taken during one 24-hour period in each month when sufficient ice covered the lake. During freezeup in December and spring thaw in May, unsafe ice conditions made sampling impossible. As before, each haul across the transect yielded four samples which were preserved separately. Because sampling was limited to the single available transect during the winter, the number of hauls taken in 1 day was limited to two since the majority of the shrimp would have either been captured or sufficiently disturbed to invalidate further sampling in the area. Also, the glacial flour sediments would undoubtedly be disturbed by repeated hauls.

Individual net samples varied greatly in size. They ranged from 1 mysid to over 18,000. Subsampling was necessary to handle the large number and volume of samples. Small samples were entirely analyzed while large samples were subsampled. A modified Waters subsampler [37] was used to facilitate counting large samples.

Following subsampling, size and sex data were recorded for *Mysis* for each separate net sample. A classification system similar to that used by Reynolds and Degraeve [29] was used. The mysids were measured from the tip of the rostrum to the tip of the telson, excluding setae. Size was recorded in this manner: mysids from 10.00 to 10.99 mm were recorded as 10 mm.

Mysids were classified into the following five categories according to sex characteristics: juvenile, immature male, immature female, mature male, and mature female.

Juvenile *Mysis*, shorter than 10 mm in length, had no distinguishing sexual characteristics. The first characteristic that develops from which males can be distinguished is a conical process on the distal end of the third segment of the antennular peduncle. It is minute in young developing males, but becomes well developed and setiferous in mature males. Mature males have the fourth pleopod extended with a visible endopod and exopod. Mature males in breeding condition have a delicate extension of the last segment of the exopod which may extend past the end of the telson.

Female mysids form a brood pouch out of four ventral oostegites which are outgrowths from the coxal joints of the seventh and eighth thoracic segments [28]. These are very light colored and minute when first recognizable in immature females. Mature females have well developed oostegites, with the posterior pair larger and overlapping the anterior pair and mottled with contracted chromatophores. The brood pouch is shaped and tightly closed with no brood visible. Brooding females have oostegites hyline, fully developed and having contracted chromatophores expanded arborescently over the lateral surfaces. The brood pouch is firm and distended and filled with either eggs, embryos, or larvae [29].

Female mysids in mature breeding condition were recorded, along with the stage of development of the brood. Berrill [30] gives a detailed account of the development of the embryos of *Mysis relicta*. In the present study, four stages of brood development included: (1) eggs present, (2) embryos present and elongated, (3) embryos with appendages present, and (4) larvae present. Larger females which had previously released the brood were also noted.

Data collected for each individual net sample included total number of *Mysis*, volume of water sampled, number of *Mysis* per litre, and size and sex frequency of the catch. These data were used to determine: (1) vertical migration, (2) size and sex frequency at different depths, and (3) in a pooled form for the total monthly size frequency analysis.

The data were used to determine the extent, pattern, and timing of vertical migration over 1 year. Vertical-migration kite diagrams were constructed by determining the percentage of the total number caught per haul that were simultaneously present at each of the four depths (figs. 2 through 7). Temperature and dissolved oxygen profiles were plotted to determine any effect on vertical migration.

The purpose of determining size and sex frequency over depth was to determine the makeup of the migrating population. Size frequency for each individual net sample was recorded as the relative percent of the total catch of the net represented by each millimetre size class. The portion of each size class represented by different sex and maturity classes was calculated to give a size and sex frequency analysis at the surface, two intermediate depths, and the bottom (figs. 8 through 16). On these graphs the juvenile, immature males, and immature females are grouped as a single entity under the heading "juveniles." Thus, the three sex stages shown are juvenile, male, and female. The number of each sex category present and the percentage of the sample represented by each sex category are given to determine whether the sample is dominated by a certain group. From calibration data for the flowmeters and the number of revolutions recorded by the flowmeter, the number of litres of water in each sample was calculated and the number of mysids per litre for each net sample was recorded (figs. 8 through 16).

A monthly size-frequency analysis was made to determine population structure, recruitment periods, life cycle, and growth. All sizes and

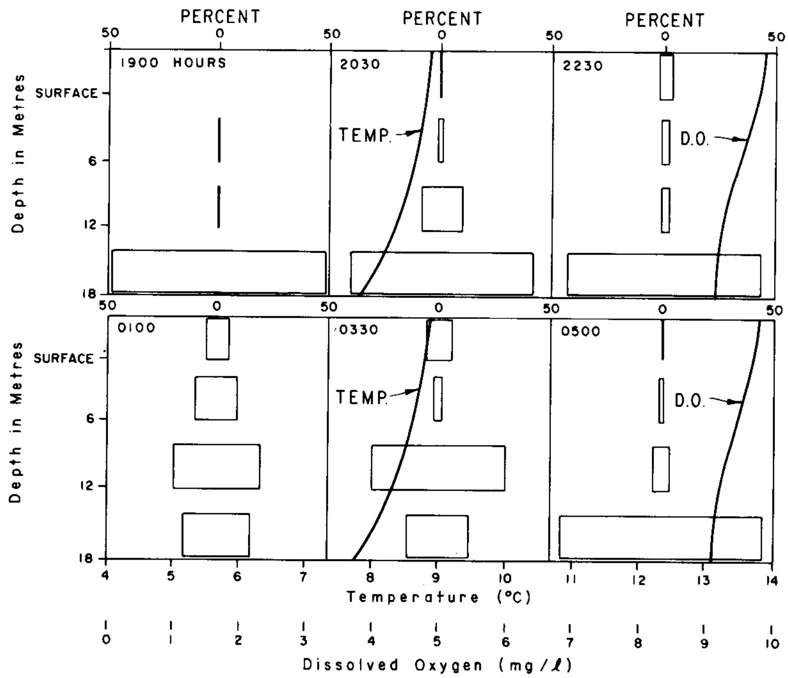

Figure 2.–Vertical migrations of *Mysis* for June 7, 1975. The width of each bar indicates the percentage of the total haul captured at each depth. Temperature and dissolved oxygen profiles are plotted versus depth.

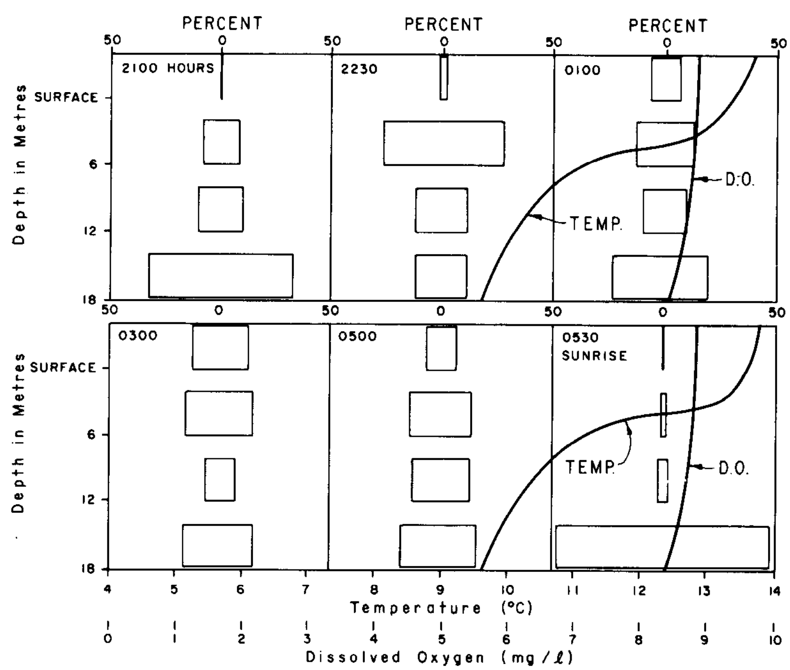

Figure 3.–Vertical migrations of *Mysis* for July 16, 1975. The width of each bar indicates the percentage of the total haul captured at each depth. Temperature and dissolved oxygen profiles are plotted versus depth.

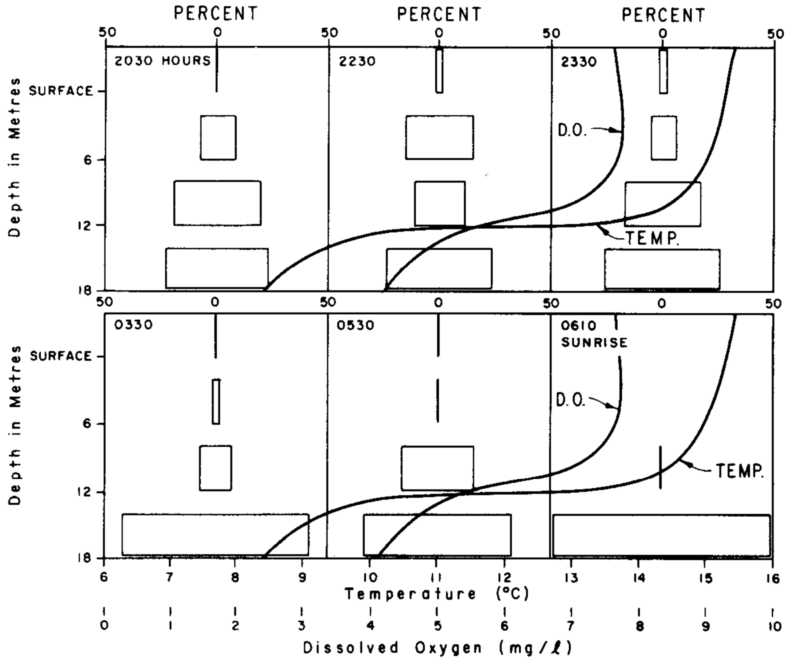

Figure 4.–Vertical migrations of *Mysis* for August 8, 1975. The width of each bar indicates the percentage of the total haul captured at each depth. Temperature and dissolved oxygen profiles are plotted versus depth.

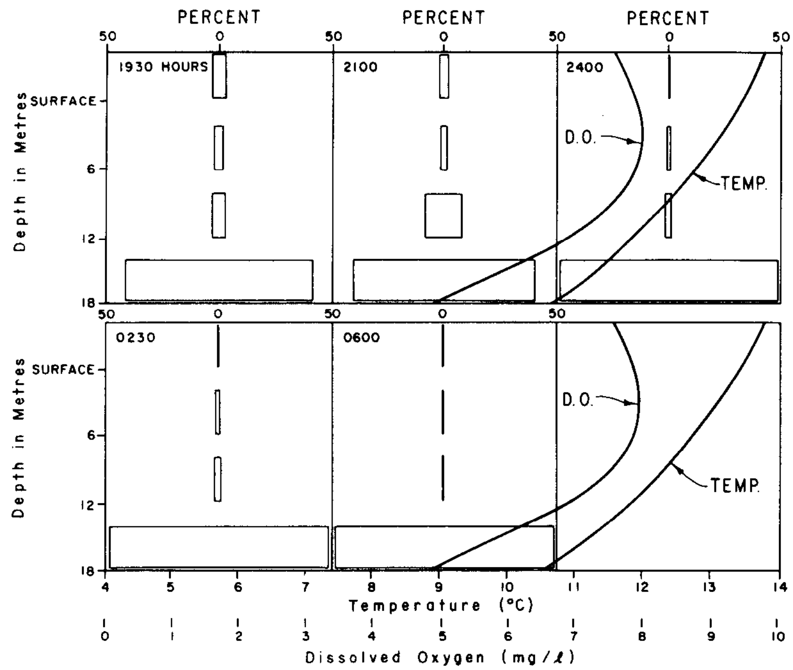

Figure 5.–Vertical migrations of *Mysis* for September 28, 1974. The width of each bar indicates the percentage of the total haul captured at each depth. Temperature and dissolved oxygen profiles are plotted versus depth.

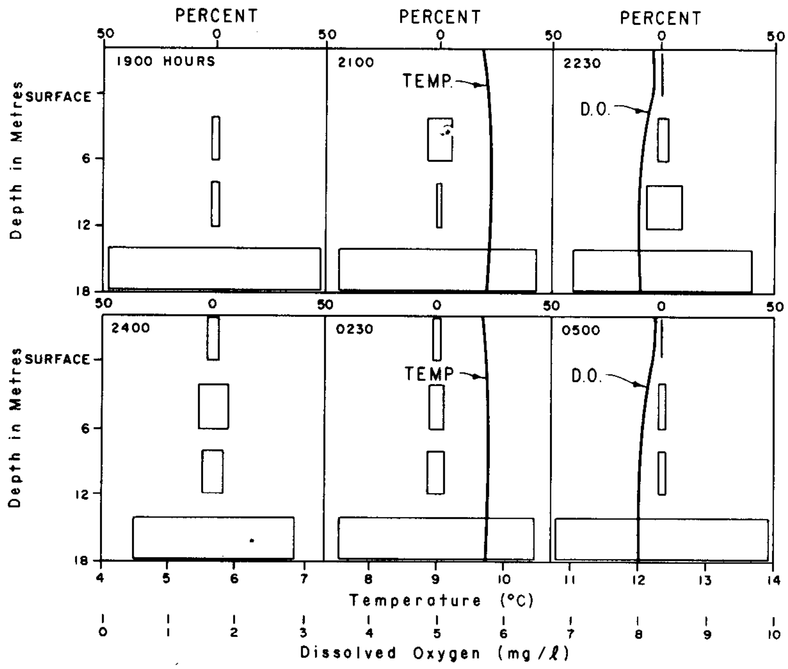

Figure 6.–Vertical migrations of *Mysis* for October 25, 1974. The width of each bar indicates the percentage of the total haul captured at each depth. Temperature and dissolved oxygen profiles are plotted versus depth.

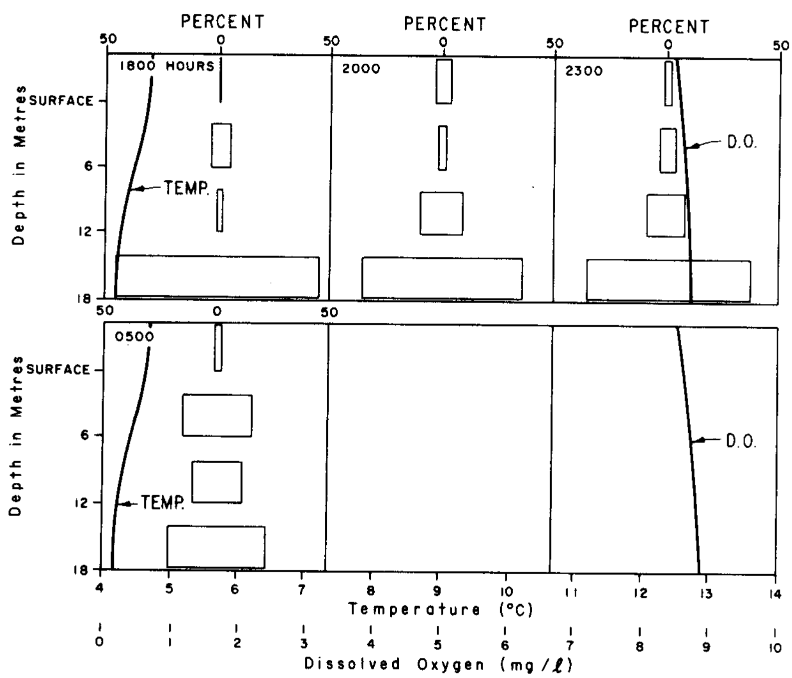

Figure 7.–Vertical migrations of *Mysis* for November 11, 1974. The width of each bar indicates the percentage of the total haul captured at each individual depth. Temperature and dissolved oxygen profiles are plotted versus depth.

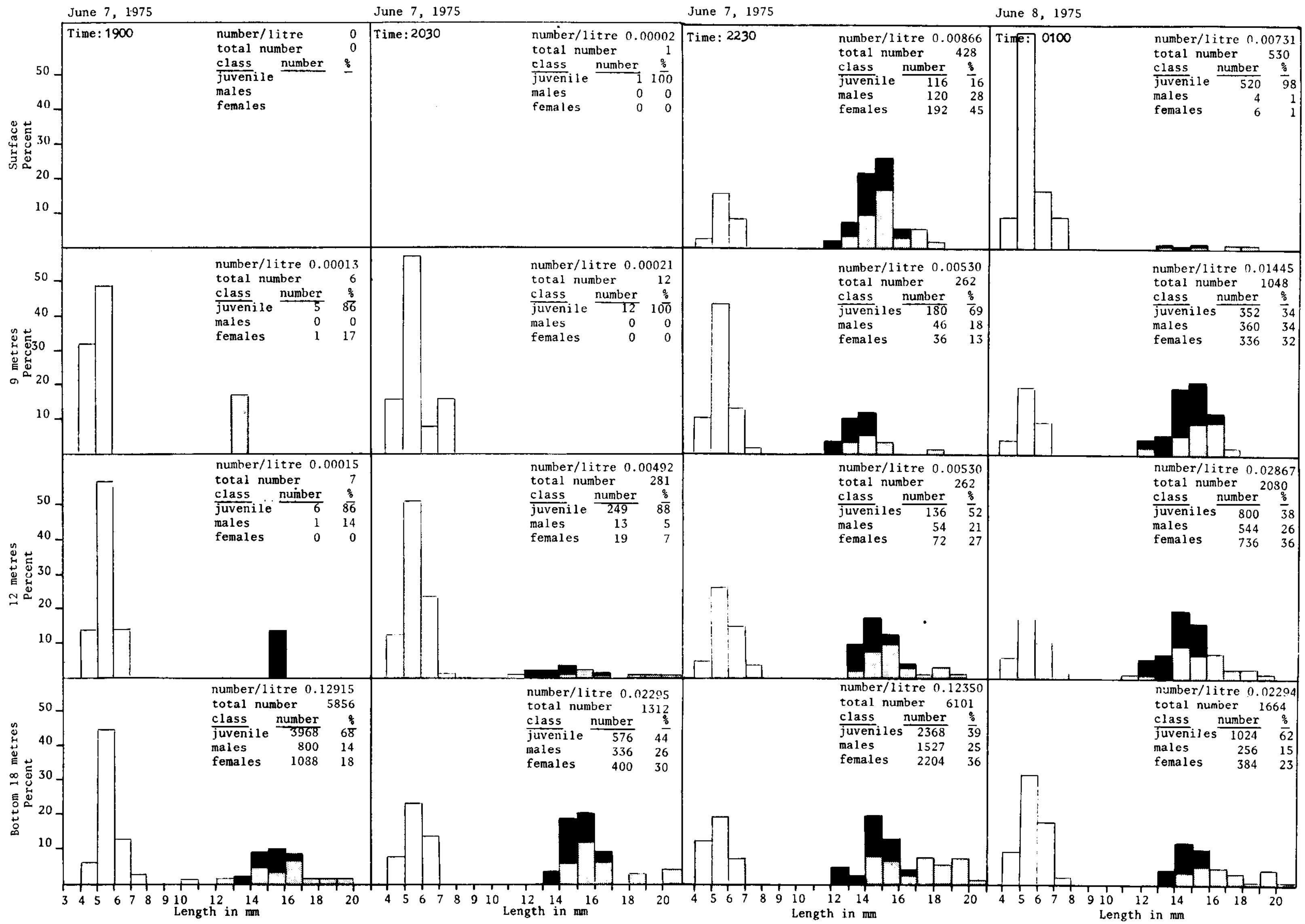

Figure 8.–Size frequency of *Mysis* captured in individual net samples at four depths. The first four samples taken during the night of June 7, 1975, are shown. Kite diagrams of these data are given in figure 2.

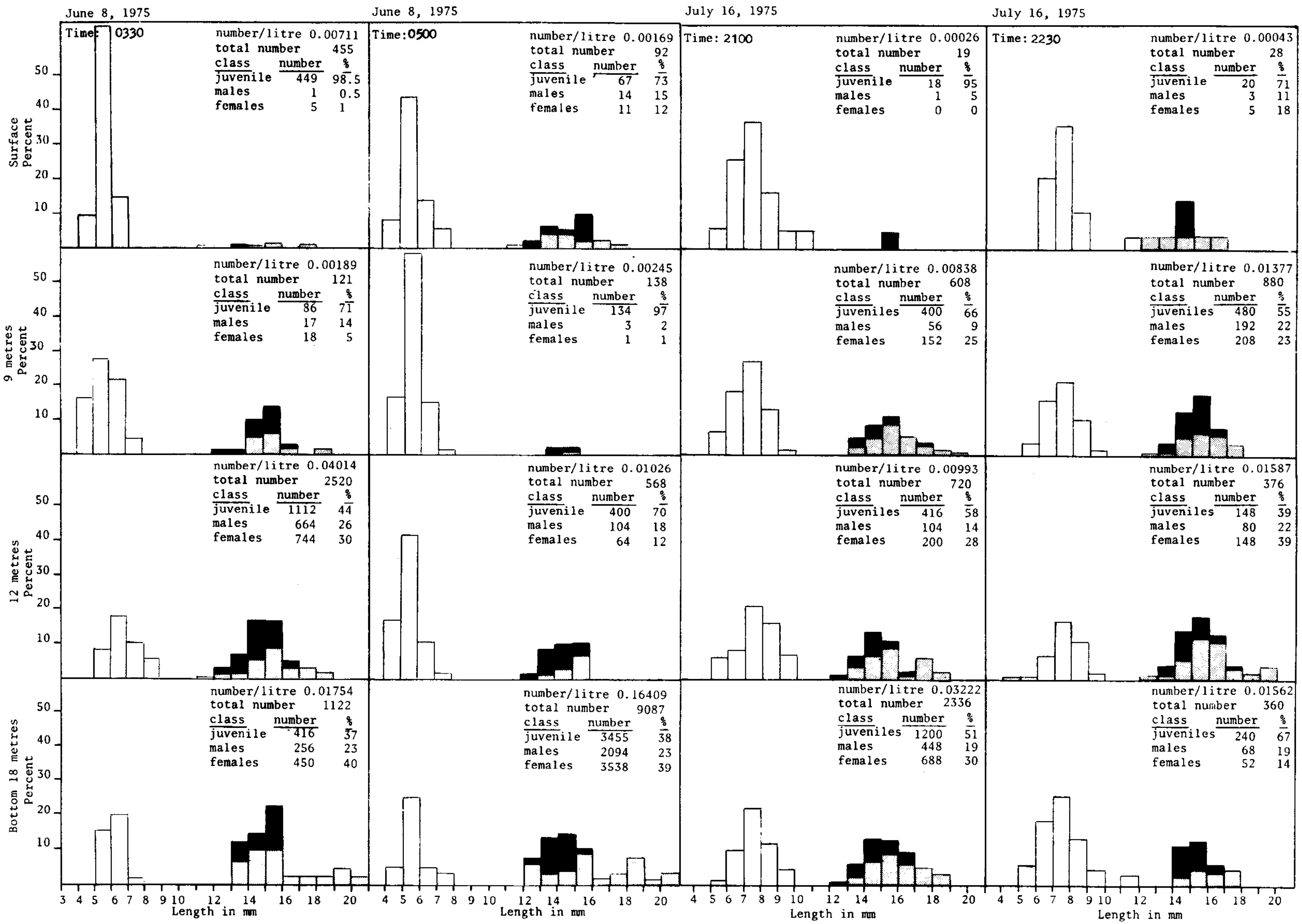

Figure 9.–Size frequency of *Mysis* captured in individual net samples at four depths. The last two samples taken during the night of June 7, 1975, and the first two samples taken during the night of July 16, 1975, are shown. Kite diagrams of these data are given in figures 2 and 3.

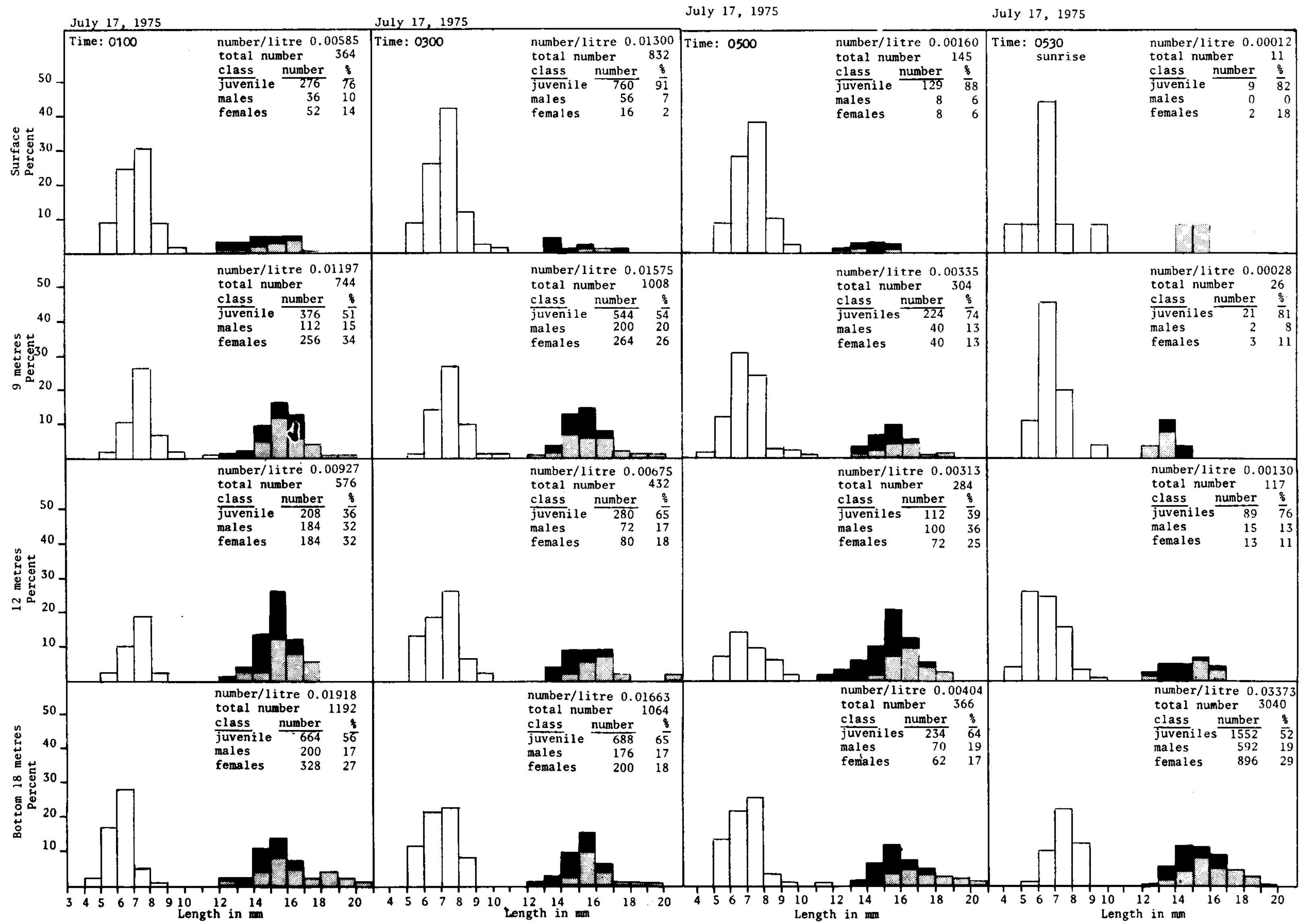

Figure 10.–Size frequency of *Mysis* captured in individual net samples at four depths. The four samples shown were taken during the night of July 16, 1975. Kite diagrams of these data are shown in figure 3.

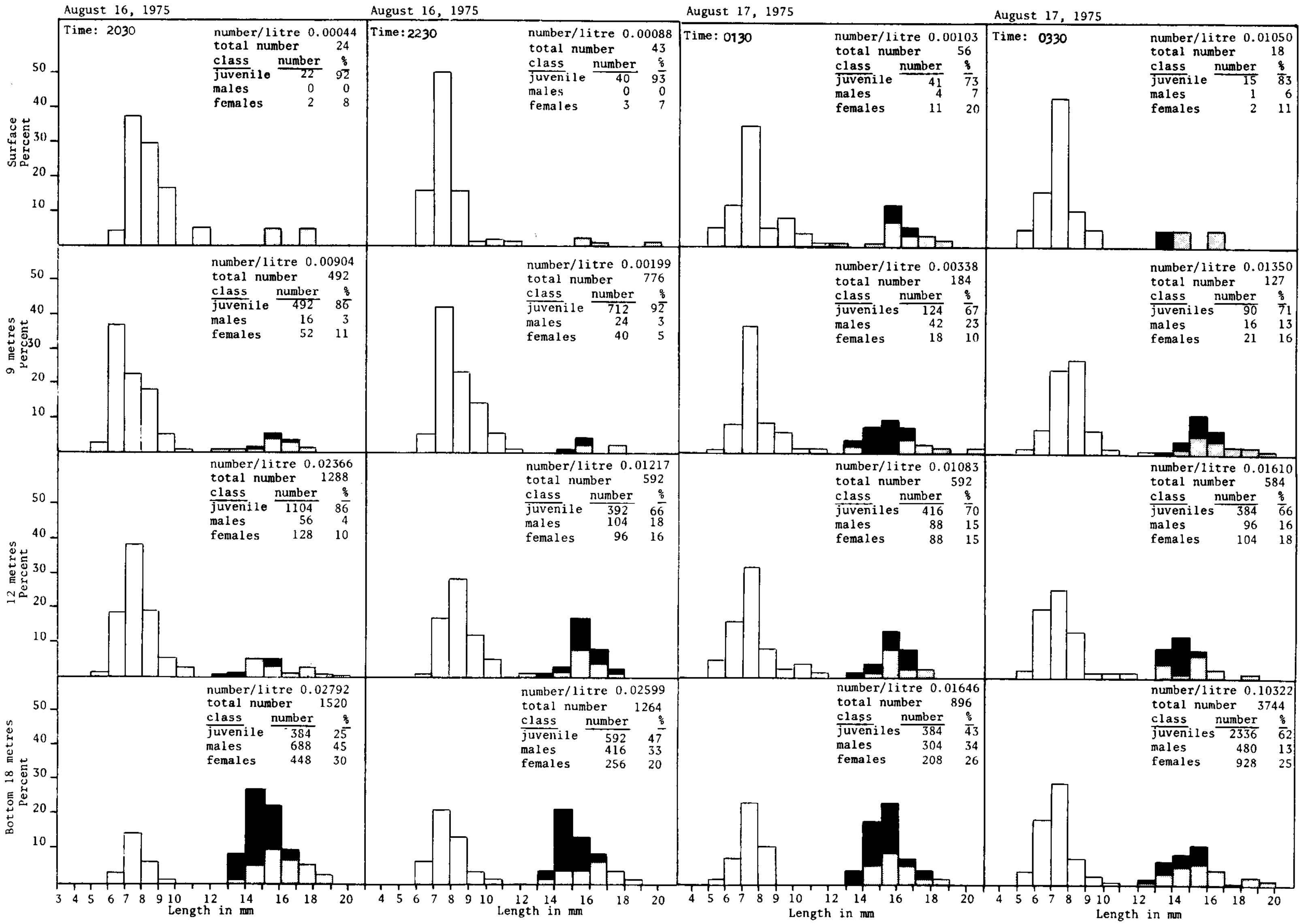

Figure 11.–Size frequency of *Mysis* captured in individual net samples at four depths. The first four samples taken during the night of August 16, 1975, are shown. Kite diagrams of these data are shown in figure 4.

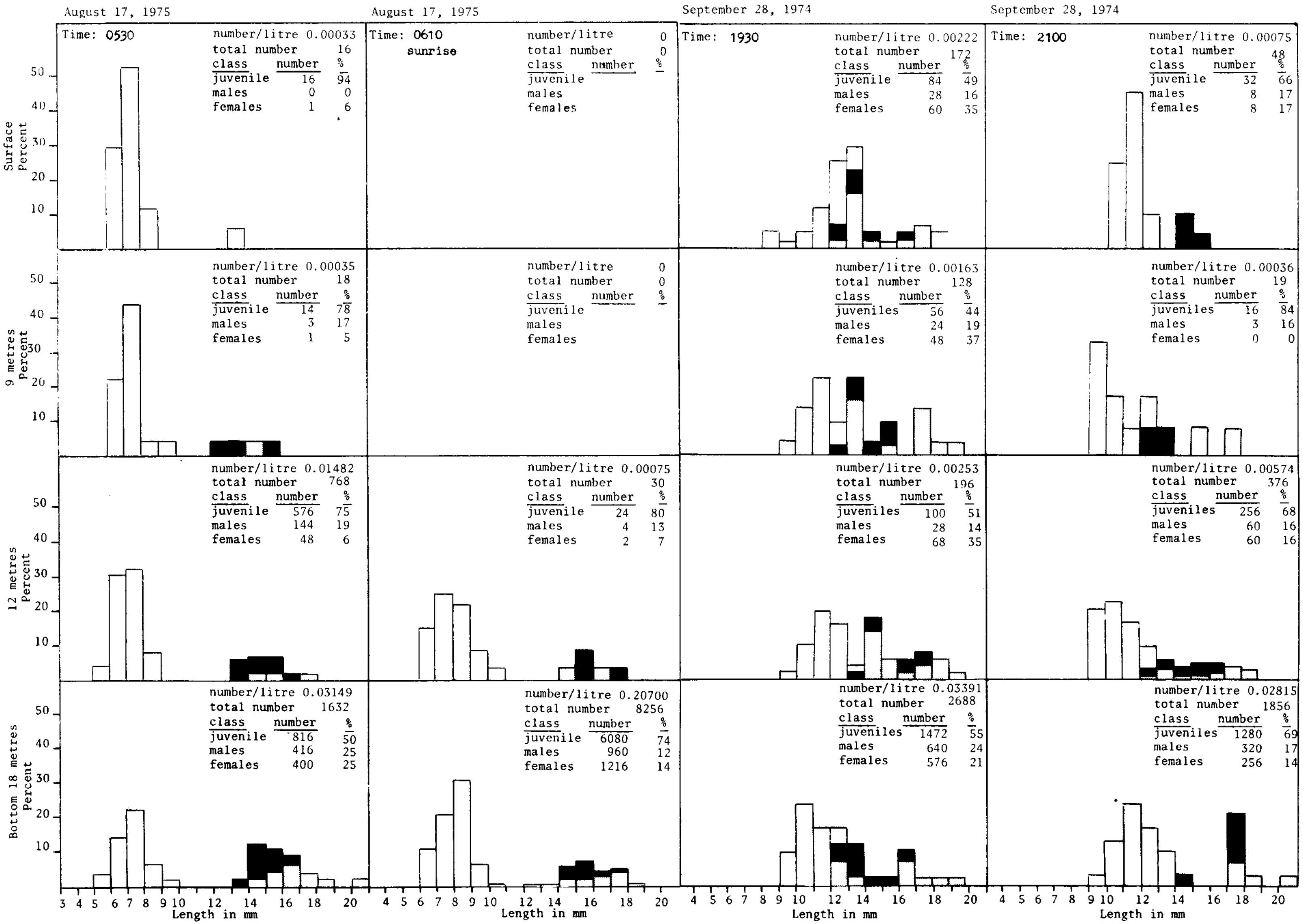

Figure 12.–Size frequency of *Mysis* captured in individual net samples at four depths. The last two samples taken during the night of August 17, 1975, and the first two samples taken during the night of September 28, 1974, are shown. Kite diagrams for these data are given in figures 4 and 5.

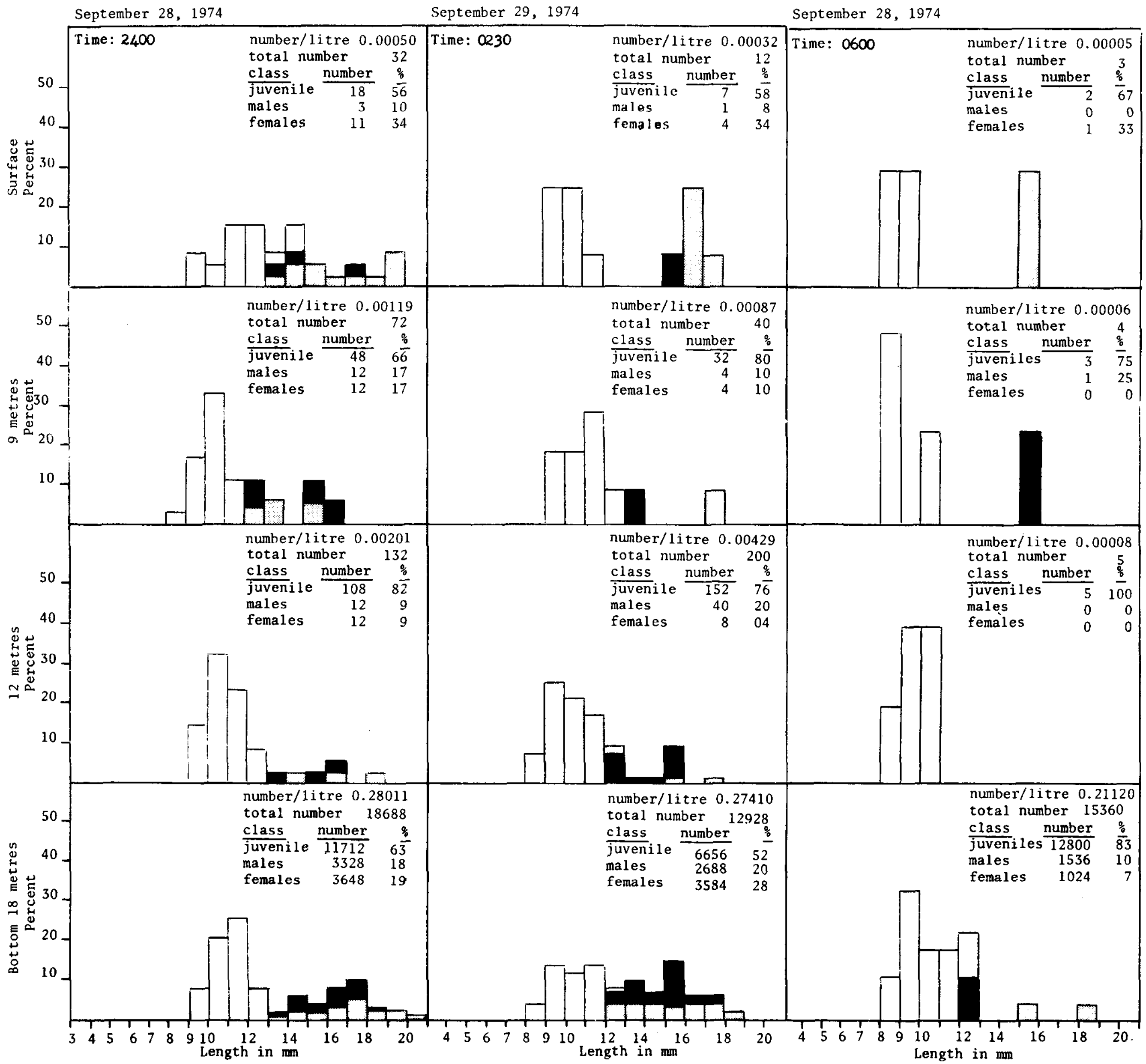

Figure 13.–Size frequency of *Mysis* captured in individual net samples at four depths. The last three samples taken during the night of September 28, 1974, are shown. Kite diagrams of these data are given in figure 5.

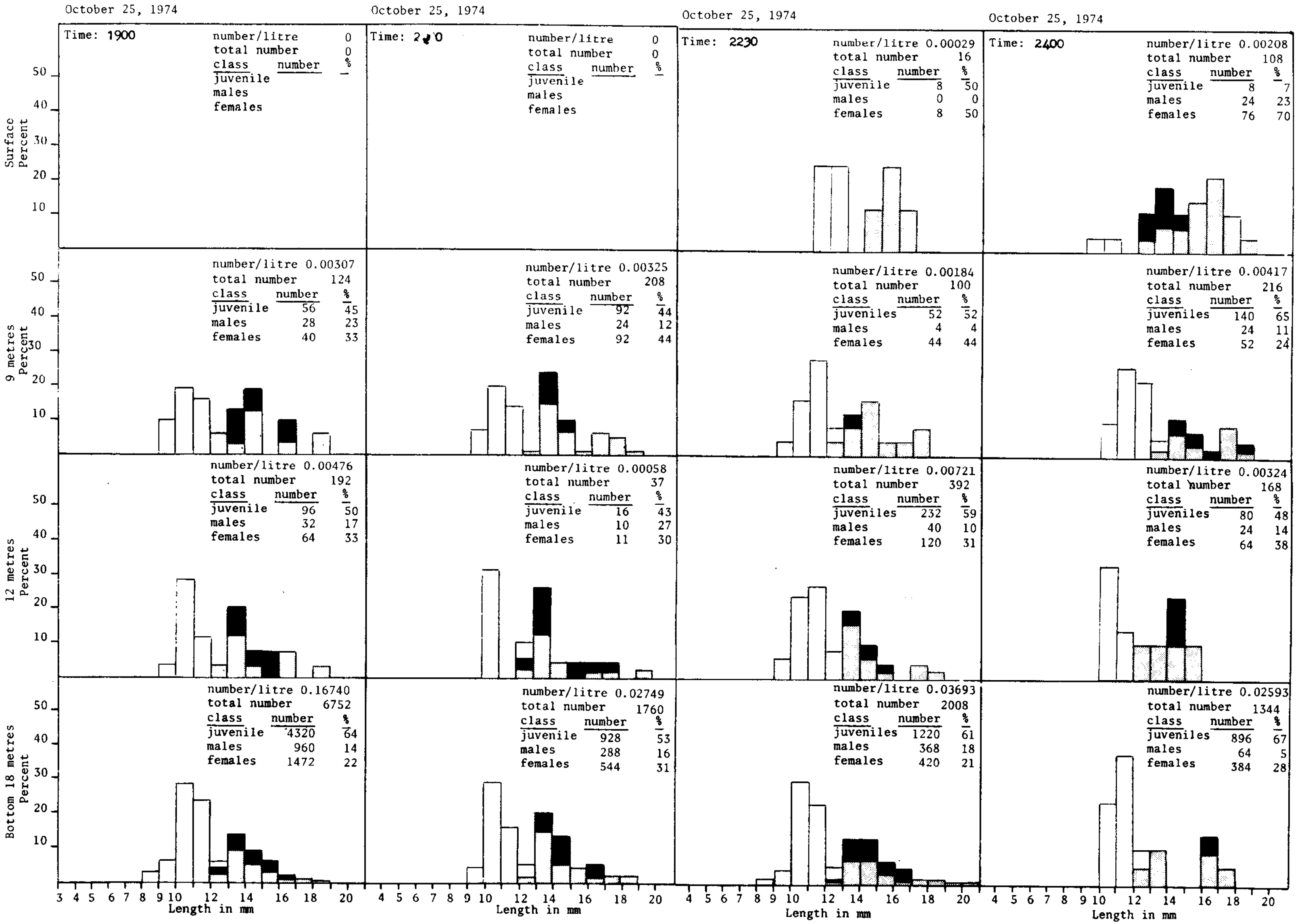

Figure 14.–Size frequency of *Mysis* captured in individual net samples at four depths. The first four samples taken during the night of October 25, 1974, are shown. Kite diagrams for these data are given in figure 6.

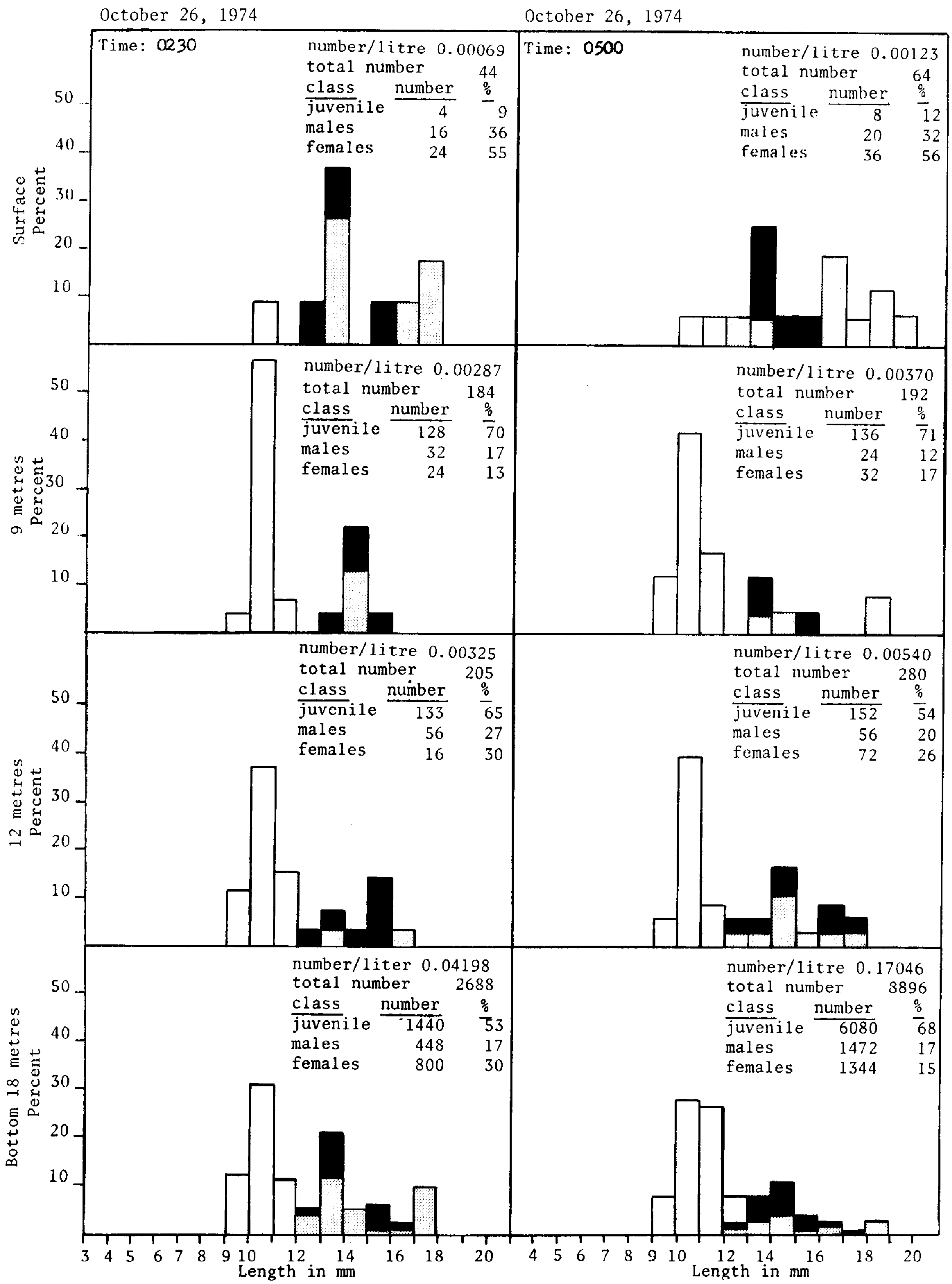

Figure 15.–Size frequency of *Mysis* captured in individual net samples at four depths. The two samples shown were taken the night of October 25, 1974. Kite diagrams for these data are shown in figure 6.

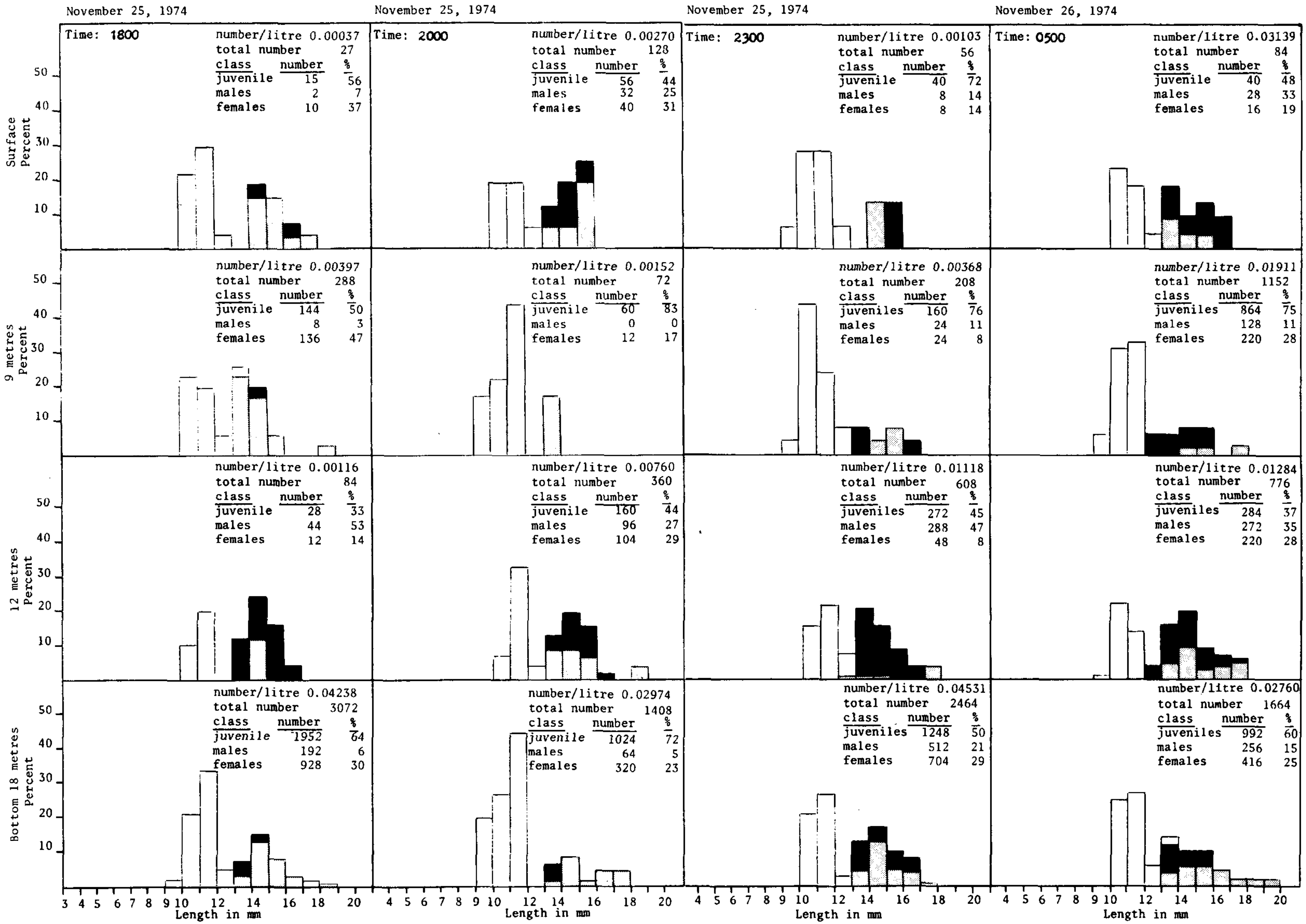

Figure 16.–Size frequencies of *Mysis* captured in individual net samples at four depths. The four samples shown were taken on the night of November 25, 1974. Kite diagrams for these data are given in figure 7.

sexes should be represented in the sample in proportion to their occurrence in the population. That is, all segments of the population, whether they inhabit the benthic, midwater, or surface areas, should be subject to capture and subsequent representation. For this reason monthly size-frequency analysis was accomplished by pooling the analyzed data from all individual samples taken during the one monthly sampling period. The total monthly size frequencies were given as the relative percentage of the sample represented by each milimetre size class. The proportion of these size classes represented by each sex and maturity level was calculated. In this case five classifications for sex were maintained as described earlier. These data are presented in the section on life histories.

Results

Samples taken in June 1975 contained large numbers of young-of-the-year mysids. The previous year class had closed ranks with the 2-year-old adults. These 1- and 2-year olds now made up the mature males and females, while the young-of-the-year were represented as juveniles. Temperature stratification had begun in early June and D.O. (dissolved oxygen) was high at all depths. These samples were taken 2 weeks after the ice had gone off the lake. Sample hours are given according to local time (m.d.t. or m.s.t.).

The migration began with small numbers of juveniles migrating to depths of 6 and 12 metres. The migration of adults was slower in the beginning. The 6-metre sample at 2030 hours shows the adults beginning to migrate. By 2230 hours, the mysids have become distributed at all levels in the water column. Samples taken at 2230, 0100, 0330, and 0500 hours show a variation in the size groups represented. The 2230-hour sample at the surface is dominated by adults, in contrast to surface samples taken at 0100 and 0330 hours which are dominated by juveniles. This suggests an age-dependent grouping. Repeated samples in one area in a short time interval could establish this more accurately. It appears that juveniles can and do appear in groups. A possible reason is found in samples from 0100 and 0330 hours. The adults are prevalent in the water column, but not at the surface, possibly resulting from greater sensitivity to temperature or light in adult mysids. Juveniles, being less sensitive, would migrate the entire distance to the surface and remain there, while the adults reached the surface (as in the 2230 sample), and then descended to the lower level as in the 0100 and 0330 samples.

The greatest percentage of the population migrated at 0100 and 0330 hours (fig. 2). The migration in June was larger in both numbers per litre and percentage of the population migrating than was seen in September, October, or November (figs. 2, 8, and 9).

During July, longer days and later sunsets delayed the mysid vertical migration until approximately 2100 hours. A distinct thermocline was evident at this time and dissolved oxygen remained sufficient at all depths. The migration began as it did in June with juveniles reaching the surface first. These young mysids reached the surface waters first and remained there throughout the night. The juvenile mysids were also the last to descend at dawn. Small numbers of migrating adults reached surface waters, but the majority of the mature mysids remained below the thermocline which was evident between 4.5 and 6 metres. Migrations involved a large percentage of the population, and the average numbers of shrimp migrating were similar to those for the month of June. A unique observation was made at 2400 hours. The night was very dark and the lake surface was completely calm. Mysids were observed swimming or resting at the lake surface. They came so far as to actually contact the surface film. When a beam of light was directed at a mysid, it would remain motionless for several seconds and then quickly dart toward the bottom. *Mysis* utilized an abdominal reflex reaction to vanish from sight with a speed that had not previously been observed.

A larger percentage of the total population is involved in the migration during July than during months in the fall. No notable differences were observed in size or sex composition of samples taken from 6 metres to the bottom throughout the night in July (figs. 3, 9, and 10).

Lower Twin Lake was strongly stratified in August. Dissolved oxygen was beginning to be depleted in the hypolimnion. August vertical migrations began at 2030 hours. Again, large numbers of juveniles migrated first and again adults did not reach the surface. Mysids were more numerous below the thermocline than above. Only a small number of juveniles occupied the surface waters. The number of mysids reaching the surface was significantly smaller than in previous months. No *Mysis* were sighted on the lake surface even though the night was very dark and the lake surface completely calm. Throughout the August sampling night, the number of mysids captured increased progressively with the depth of the sample. In all samples, the greatest relative percentage of shrimp occupied the benthic zone. Corresponding kite diagrams were pyramid in shape. Sunrise (0610) found the mysids retreating very rapidly toward the bottom. Only a small number were found in the water column, and that was at the 12-m level (figs. 4, 11, and 12).

Vertical migration during September was less than at any other time sampled. The majority of the population remained on the bottom throughout the night (fig. 5). The greatest portion of the migration occurred immediately following sunset. The first surface sample contained a large number of mysids relative to other surface catches. Surface numbers decreased steadily as the night progressed. *Mysis* apparently entered the epilimnion early and retreated to depths of 6 metres or more. Following the initial ascent, the greater number of mysids were collected at the 12-m level from 2100 to 0230 hours. Water temperature decreased at a constant rate from surface to bottom. A bottom temperature of 10.6 °C was near the yearly high for that depth. Bottom D.O. was becoming depleted, especially in the center of the lake, where it reached below 2 mg/*l*. Dissolved oxygen in the sample area did not drop low enough to affect the *Mysis*. Size and sex composition of the surface population was similar to that of the bottom population. At dawn, juvenile mysids were the last to return to the bottom (figs. 5, 12, and 13).

The lake had undergone fall overturn prior to the October sampling. The lake was isothermal at 8.0 °C and dissolved oxygen was greater than 7 mg/*l* at all depths. *Mysis* migrations increased during October. The early rapid rise to the surface noted in the previous month was not evident; no mysids were taken at the surface prior to 2230 hours. At this time mysids arrived at the surface and remained there until dawn. The number of mysids per litre showed larger numbers in the water column and smaller numbers on the bottom than in September, but the migrators were outnumbered by mysids remaining at the bottom. Mysids were found in greater numbers at 12- and 6-m depths than at the surface. Sex and size distribution was relatively constant, with a notable exception occurring in surface catches at 2400, 0230, and 0500 hours, where juveniles represented a much smaller percentage of the sample than normal. Mature females dominated these samples with a larger than normal percentage of mature males also being present. Three consecutive samples of this makeup, particularly because each contains a majority of large females, suggests a possible social behavior. These samples were collected during breeding season and they may possibly indicate a breeding swarm or merely an increased movement of mature *Mysis* during the period. *Mysis* remained in the water column throughout the night and retreated at sunrise (figs. 6 and 14).

Water temperature during November was isothermal at 4 °C and dissolved oxygen was very near saturation at all depths. Vertical migrations began immediately following sunset. The number of shrimp in the water column increased as the night proceeded. Only four samples were collected because of inclement weather. The greatest number of mysids taken from the water column were captured at the 12-m level. Smaller numbers were collected at the 6-m level and at the surface. The largest numbers were collected just before sunrise. Size and sex composition of the sampled population did not show any notable differences with time or depth. Samples included representatives of juveniles, males, and females in all but one case. Mysids were more abundant at all depths in the water column than at any other month during fall 1974 (figs. 7, 15, and 16).

Discussion and Conclusions

Vertical migrations are a common phenomena and take place during all open-water months. Mysids occupied the water column during the entire night in varying numbers; however, the intensity of migrations varied greatly. Migrations were greatest in the summer months of June, July, and August, followed by a sharp decrease in September. A slight increase took place in October and, by November, vertical migrations were again high, being only slightly below summer levels.

The bed of the tailrace channel will be at a depth of 7.6 metres when the lake is at its current average surface level of 2797 metres. Depending on the month and time, *Mysis* were found at this depth in large numbers. In many cases, some mysids occupied this area most of the night. When pumping occurs during hours of darkness, some mysids will be carried into the powerplant. The degree of entrainment will vary with factors such as season, thermal conditions, and ambient light levels at the critical depth.

Beeton [18], Brownell [28], and Teraguchi [23] found light and temperature to be the most important factors controlling mysid migrations. Thermal gradients modify the intensity of expression of the response to illumination. The results of this study agree with these previous conclusions.

Migrations coincided with changing light intensities, beginning progressively later as day length increased. Following summer solstice, mysids began ascending earlier each evening and decending later each morning. Juvenile mysids began migrations earliest. The majority of mature mysids reached the upper strata only after darkness. The midnight sinking and dawn rise phenomena described for crustacean migrations by Cushing [20] were not exhibited by *Mysis* in Twin Lakes. Beeton and Brownell found similar behavior for *Mysis relicta*.

Thermal gradients influence adult mysid migrations. Very young mysids showed little behavioral modification in regard to temperature profiles. They migrated actively into warm surface waters. Juveniles were found at all depths, but made up the largest percentage of the population at the surface. They reached the surface first, remained there the longest, and descended last. During June, July, and August, mysids from 3 to 8 mm dominated the surface samples. Beginning in September, this domination of surface samples ended, possibly because mysid sensitivity to temperature changes with increasing maturity [23]. Beginning in October, with fall overturn, the makeup of surface samples changed completely.

Earlier in the year, mature mysids had avoided warm surface waters, but in June, large numbers of mature mysids made a brief appearance at the surface (2230 hours). By 0100 hours the majority had returned to 6 to 12 metres and by 0330 hours they were concentrated at the 12-m level. In July and August, only a very small percentage of mature mysids reached the surface. The majority were in the 6- to 12-m strata. In September, some mature mysids came to the surface, but again remained only briefly. The juveniles no longer remained at the surface in large numbers, possibly due to an increased sensitivity to temperature. With fall overturn and isothermal temperature conditions, migration patterns changed drastically. As is evident from October samples taken at 2230, 2400, 0230, and 0500 hours, mature mysids now dominated the surface samples. The temperature barrier no longer prevented mature mysids from reaching and remaining at the surface. The possibility of a social interaction triggered by the breeding season cannot be overlooked. At no other time were concentrations of large females found at the surface. During October, females dominated the surface samples from 2230 to 0500 hours. In November, with water isothermal at 4 °C, vertical migrations showed no patterns with respect to individual maturity levels.

LIFE HISTORY

Introduction

Knowledge of the life history of *Mysis* was essential in determining the role of mysids in the Twin Lakes ecosystem. Aspects of the life cycle have been well documented in the literature [19, 28]. Variations in recruitment, growth, longevity, and breeding season are common among different populations.

A generalized scheme for the life cycle of *Mysis relicta* can be obtained from the literature. The young are usually released from the brood pouch in the spring at a length of 3 to 4 mm. Growth averages 1 mm per month. *Mysis* become sexually identifiable at 8 to 11 mm, with females growing faster and becoming distinguishable as a separate and larger size class exceeding 16 mm in length. Males grow slower and attain a maximum size of 16 mm. Breeding takes place in colder months and the males die within several months after breeding. Females can only be impregnated during ecdysis. Eggs laid in the marsupium are held for 3 to 4 months as they develop into larvae. The juvenile mysid that escapes from the brood pouch looks and behaves like a miniature adult and is capable of swimming and feeding immediately upon hatching [30].

Lasenby and Langford [17] found that temperate mysids are released in May, mature in one summer, breed in the fall, and produce a new generation by the following May. Males then die and females live a second year. Reynolds and Degraeve [29] reported a similar 1-year life cycle for *Mysis* in southeastern Lake Michigan. They found a similar peak of recruitment in May, but also that breeding may continue to a lesser extent all year. These mysids grew quite rapidly with monthly growth rates of 1.7 mm between January and April. Average life span was 12 months.

In contrast, a 2-year life span has been reported in several studies. Lasenby and Langford found in an arctic lake that mysids were released from the brood pouch when they are 3.5 to 4.0 mm long. After approximately 12 months they separated into two size classes and, by September, when they were approximately 18 months old, the smaller animals became mature males and the larger became mature females. In Great Slave Lake, Larkin [9] found that *Mysis* took 2 years to mature.

The reproductive season varies with different populations. Thienemann [38] found mainly winter reproduction and concluded that summer reproduction was unpredictable from one lake to another. Furst [7] suggested that in some lakes in Sweden there may be two populations living together, but separated by breeding times. Results of studies in Lakes Huron, Ontario, and Superior agree [39]. The mysid population structure varies greatly between these lakes. Recruitment in Lake Superior occurs during the spring, with *Mysis* reaching maturity in the second year; in Lake Huron, recruitment occurs from April to early October. This could be the result of two main periods of reproduction per year, or conversely, the reproductive period may be very long. Data from Lake Ontario samples indicated recruitment in April and August, but not in November.

These examples show different possible adaptations of the life cycle by *Mysis relicta*. Recruitment, growth, longevity, and breeding season are modified by individual populations in relation to their specific environment. These life history parameters were examined for Twin Lakes mysids.

Results

Size frequency histograms for samples collected in September 1974 through August 1975 are given in figures 17, 18, and 19. These figures were compiled from pooled data from all individual samples taken during one monthly sampling period, as described in the sampling methods section. Data for these figures are presented in table A-2. *Mysis* were identified as being representatives of one of the five sex classifications described in the sampling methods section.

Juveniles

The life cycle of *Mysis* in Twin Lakes can be followed by examining size-frequency distributions over the course of a year. Consider first the April 1975 sample (fig. 17). The large peak at 4 mm is the first appearance of young-of-the-year mysids. This sample was taken through the ice. This peak can be followed from June through August (fig. 18) as the young-of-the-year grow rapidly during the summer, reaching a maximum length of 9 mm in August. The September sample was collected in 1974, but the young-of-the-year are again apparent by the 9-mm peak. At a length of 10 mm, mysids become sexually identifiable. This age class shows a peak at 10 mm for October and 11 mm for November. No samples were obtained in December because of unstable ice conditions. By January, the peak for juveniles had merged with the mature population due partially to the very slow growth rate of mature *Mysis* during winter months. The smallest mature males may be the same length as large juveniles, but there is a definite difference in sexual characteristics when there is a 1-year age difference. This is shown in the 12-mm size class for January 1975 (fig. 19). Graphs for January and February show the juveniles, now recognizable as immature males and females, reaching maximum lengths of 12 and 13 mm, respectively. Returning to the graph for April 1975 (fig. 17), the juveniles are now 12 months old. They are easily identifiable as males and females, but are still immature. By June, July, and August, this group is 1-1/2 years of age and beginning in September they develop characteristics of mature mysids (fig. 18).

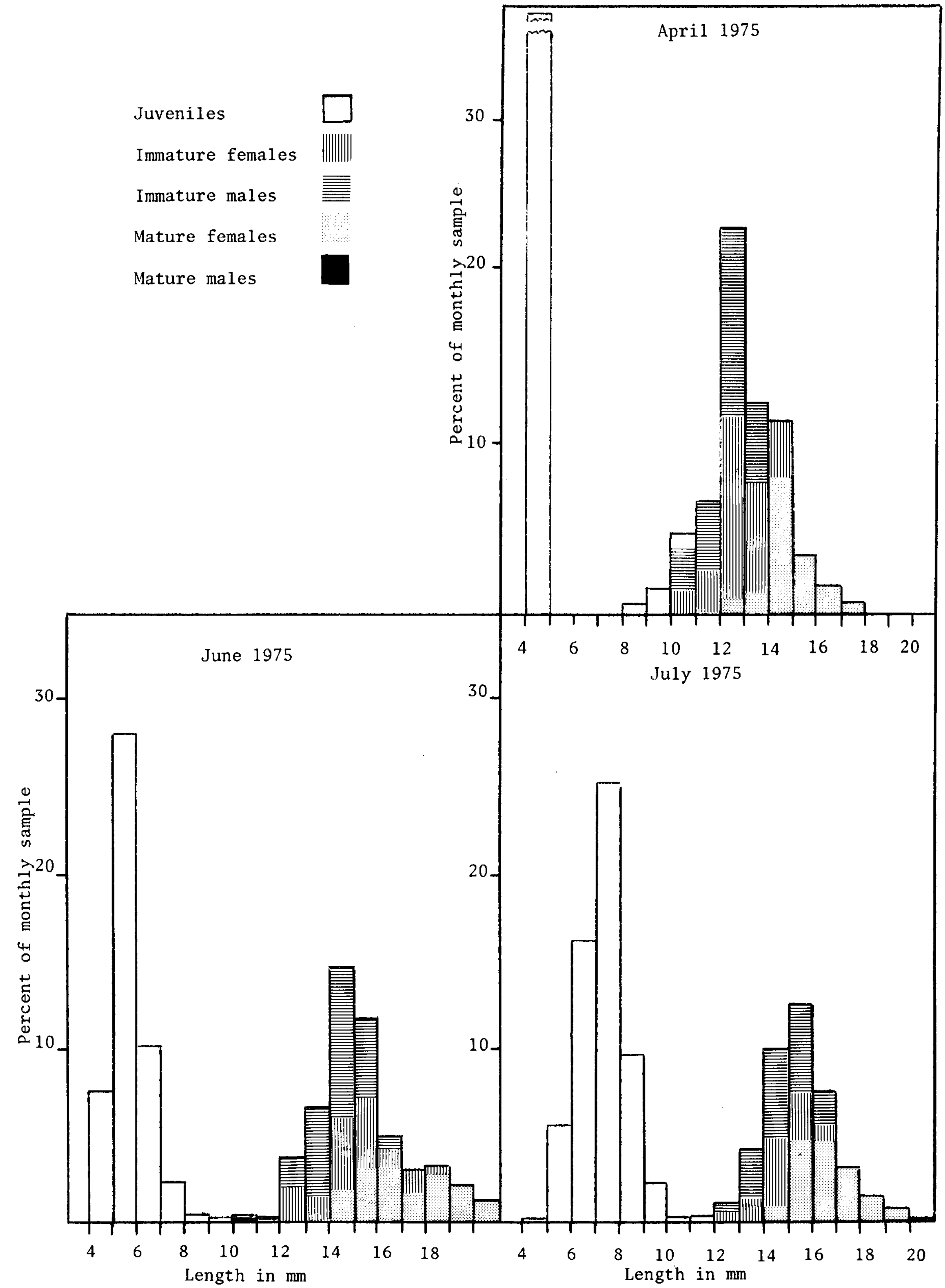

Figure 17.–Monthly size frequency for *Mysis relicta*. (April, June, and July 1975)

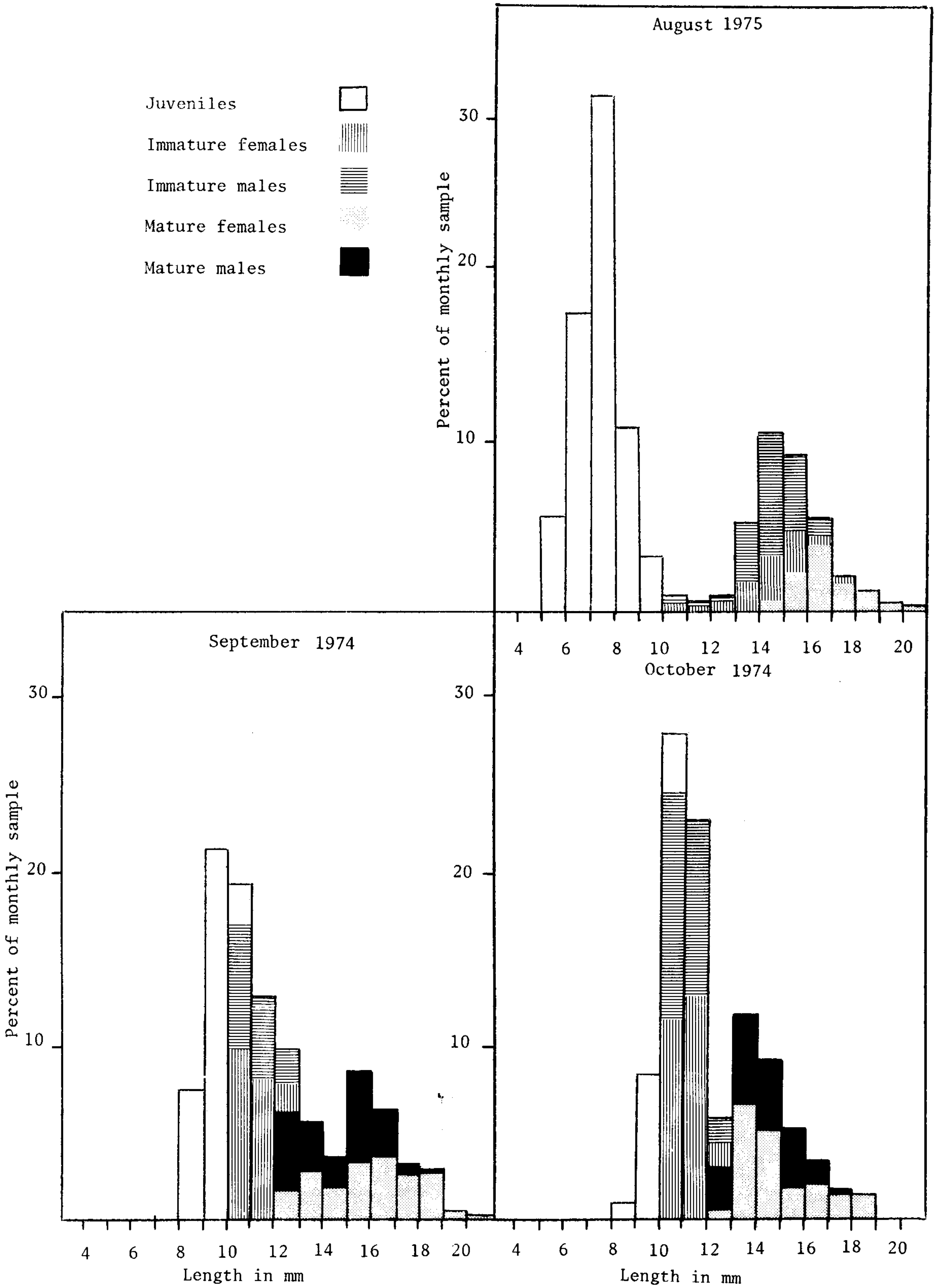

Figure 18.–Monthly size frequency for *Mysis relicta.* (August 1975 and September and October 1974)

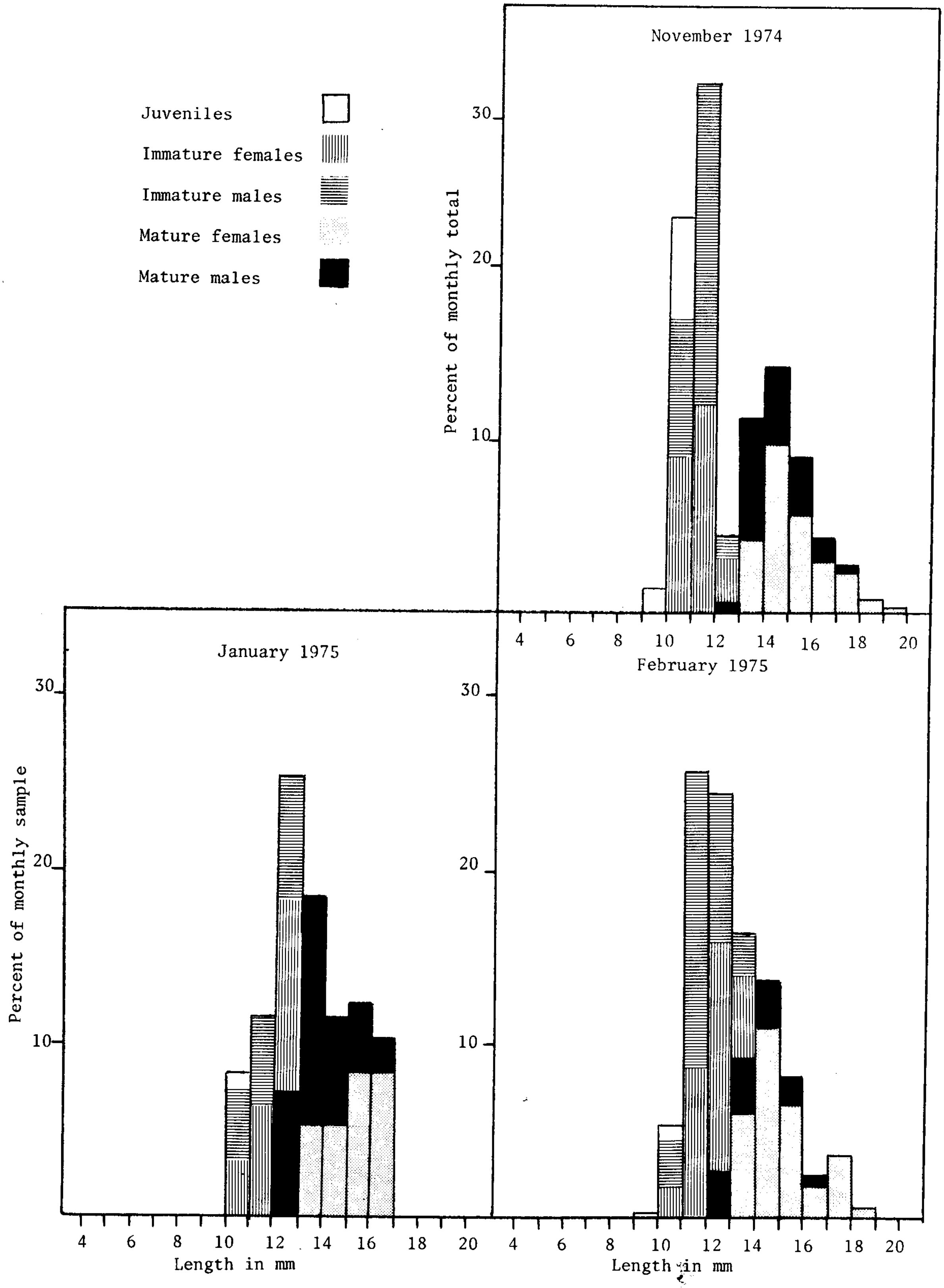

Figure 19.–Monthly size frequency for *Mysis relicta.* (November 1974 and January and February 1975)

Mature Males

Breeding characteristics become evident during October and November for mysids larger than 12 mm. Mature males breed during the fall. They are evident in the population during January and February, and by April they have disappeared completely. No mature males were found during April 1975 (fig. 17). Males die within several months after breeding, ending a life cycle thats lasts between 18 and 20 months. Maximum recorded size for males in Twin Lakes was 17 mm.

Mature Females

Females reached maturity by September at 1-1/2 years of age (fig. 18). Brood pouches develop during October and November. Mating and subsequent release of eggs into the marsupium takes place during winter months from November to January. Females are gravid during January, February, and March. Embryos in various stages of development can be found in the marsupium during April when the earliest of the young are released.

Fifty percent of females had eggs present in January; 61 percent had eggs present in February. No samples were collected during March and, by April, the first young-of-the-year were observed. Females carrying broods in April varied in stages of development from stage 2 to stage 4 (see stage description in previous section). Forty-five percent of females had released the brood, 18 percent of the broods were in stage 3 or stage 4 of development, and 11 percent were in stage 2. Only 2 percent of females still carried eggs and 2 percent were in brooding condition, but had no brood present. By June, only one female was found with eggs and two females still held larvae.

While males die after breeding, females are capable of surviving into the third year. Mature females ranging in size from 14 to 20 mm survive through the third summer. The presence of small numbers of these large gravid females in the fall suggests that some females survive to breed a second time. These 2-1/2-year-old females reached a maximum size of 22 mm. It is not known whether females in this category were successful in producing a second brood before dying off in the spring of their third year.

Discussion and Conclusions

Mysis relicta in Twin Lakes reach maturity in 16 months. They are released from the brood pouch in June and are mature after their second summer. Males live a maximum of 2 years while some females may survive well into their third year. Males die after their first breeding season; however, females may live into a second breeding season and may possibly produce a second brood. The 2-year life cycle for *Mysis* in Twin Lakes is similar to that observed in other cold oligotrophic lakes. An organism may normally take 1 year to reach maturity in temperate regions, while it would take 2 years to reach maturity in the arctic [40]. This lengthening or slowing down of the life cycle is due to decreased growth at lower temperatures and the decrease in food available. Furst [7] determined that the life cycle of *Mysis* is dependent on biological and environmental conditions. In that study mysids with a 1-year life cycle were introduced into a colder, more oligotrophic lake. A 10-year interval allowed *Mysis* to become strongly established in the new lake. The result was a decreased growth rate in the new population, with some mysids failing to reach sufficient size to become mature the first year. These mysids were unable to breed during the first fall and did not breed until the following year, when they had attained sufficient size. Observations made on the population during the next 5 years showed decreasing growth and an increasing number of mysids breeding in the second year. The decreased growth rate was believed to be the result of increasing intraspecific food competition resulting from increasing population density.

Tattersall and Tattersall [3] reported that the growth rate of *Mysis* averaged 1 mm per month, increasing during the summer and decreasing during the winter months. Growth curves for *Mysis* in Twin Lakes were obtained by plotting the average length of each cohort for juveniles, males, and females (table A-3). Growth was most rapid during the first summer, averaging 1 mm per month. During the first winter of life, growth was very slow, averaging about 0.33 mm per month. Growth rates increased the second summer to a rate of 0.5 mm per month. Lasenby [19] reported that the growth rate of mysids in Stony Lake was the highest during the summer, when food was most abundant. In Twin

Lakes, mysid growth was not evident during the second winter of life. By this time, males had reached maturity and attained maximum size. Two-year-old females showed a slight increase in growth in their third summer. Size differences between mature males and females were about 1 mm for the average length of the cohorts (fig. 20).

The growth rates and maximum sizes attained by Twin Lakes mysids indicate a relatively slow-growing and small-sized population. Growth to 14 mm took 14 months and the average growth rate for this time was 0.71 mm per month. Maximum size recorded for Twin Lakes mysids was 22 mm, with individuals larger than 20 mm being quite rare. Brownell [28] reported *Mysis* reaching a length of 30 mm in Cayuga Lake. Holmquist [22] stated the absolute size range for *Mysis* as 4 to 23 mm. Furst [41] used data on the ultimate length of males attained before death to compare growth rates for 15 different populations. He concluded that a slow growth rate coincided with a 2-year life cycle.

Successful introduction of Twin Lakes *Mysis* into Big Creek Lake, Colo., showed that growth is

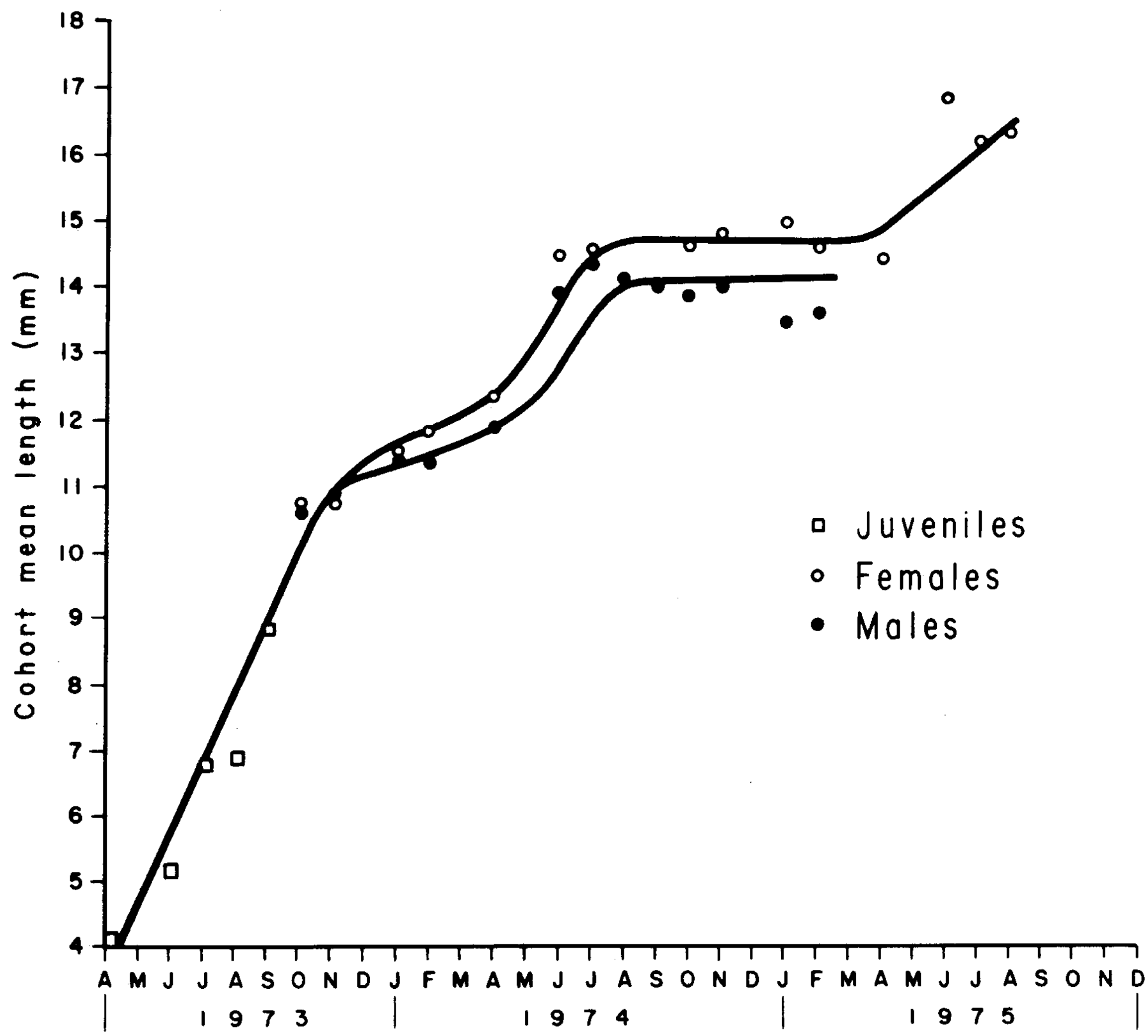

Figure 20.– *Mysis* growth curves. Points indicate the average monthly length of *Mysis* for each cohort for juveniles, males, and females. *Mysis* became identifiable as males and females at 10 mm. Variation in growth between summer and winter is apparent. The curve was drawn by inspection.

dependent on environment. Mysids are less abundant in the new lake and many have reached sizes of from 22 to 25 mm. The Big Creek Lake system has not been studied, but it is probable that growth rates and corresponding aspects of the life cycle are different in the new environment.

The reproductive season for Twin Lakes *Mysis* included fall breeding, winter brooding by females, and spring release of the young. Mysids in breeding condition were first collected in October and November. Males breed at lengths of 12 to 17 mm; females carrying broods ranged from 12 to 22 mm. Gravid females were present from January through June. Four months were required from the time eggs were laid in the marsupium until larvae were released from the brood pouch. Young mysids were 3 to 4 mm in length. April was the earliest month that mysids released their young, and by the end of June all of the young-of-the-year had been released from the brood pouch.

Lasenby [19] believed that temperature, dissolved oxygen, and food determined the reproductive period of *Mysis*. The necessary temperature conditions for breeding are found only during the winter. Breeding begins only at low temperatures, about 7 °C, and is most active at 3 to 4 °C [8]. Dissolved oxygen is replenished with fall overturn, so it would be sufficiently high during months of late fall and winter. The final factor, sufficient food, would determine whether breeding would take place. As discussed above, mysids in arctic and oligotrophic lakes took 2 years to reach sufficient size for breeding. Scarcity of food would limit growth and also might prevent mysids from storing sufficient nutrients for breeding. Holmquist [22] found *Mysis* collected in summer and fall appeared to be quite well fattened and carried large oily drops in the hepato-pancreas. Such large reserves of nutrients were necessary to manufacture the fairly large amount of sperm and eggs produced in the fall. Twin Lakes mysids required two growing seasons to reach reproductive capacity and consequently began breeding when temperatures decreased in the fall.

POPULATION DISTRIBUTION

"Mysis relicta" Population Movements

The purpose of this portion of the study was to determine the distribution pattern of the *Mysis* population and to detect spatial and temporal changes in mysid density. The homogeniety of distribution of benthic mysids was also tested. These characteristics of the population were analyzed using a monthly series of benthic trawls taken from Upper and Lower Twin Lakes. Observations made during scuba dives at the lakes were used to substantiate findings. Knowledge on population patterns, densities, and movements should prove useful to a post-operation study on the effects of the pumped-storage plant.

The horizontal distribution of a mysid population is affected by depth, water temperature, dissolved oxygen, and seasonal changes. *Mysis* survival is dependent on temperature and D.O. within a narrow range and, consequently, its distribution is limited to areas where these factors are suitable. Samter and Weltner [42] found *Mysis* only in lakes which had a colder lower stratum well supplied with D.O.

Pennak [43] believed 14 °C to be the maximum temperature that *Mysis* can tolerate for an extended time. During diurnal vertical migrations, mysids could tolerate water of 21 °C for a limited time [21]. Mysids acclimated at 9 to 14 °C had an upper thermal limit of up to 22 °C [4]. Mysid tolerance to D.O. has been shown to be directly dependent on temperature [28]. Early literature reports on lethal D.O. levels varied, probably the result of failing to consider the interactive effect of temperature and D.O. The combination of high temperature and low D.O. caused the highest mortality in mysids. Brownell found that 2 mg/*l* D.O. was sufficient for *Mysis* at 7 °C, but, as temperature increased, the D.O. requirement became greater. At 18 °C, D.O. of 8 mg/*l* was required for good survival. When the D.O. was reduced to between 1.0 and 1.5 mg/*l* at 5 °C, all mysids died. At low temperatures, the lethal

D.O. concentration would be between 1.5 and 2.0 mg/*l*.

Several reports have been given where mysids avoided or migrated horizontally away from water with D.O. concentrations below 2 mg/*l*. In Trout Lake, Wis., Juday and Birge [21] found *Mysis* abundant at a depth of 12 to 15 metres, where D.O. was 4.5 mg/*l*. From 20 m to the bottom at 35 m, *Mysis* were not found. Dissolved oxygen concentrations were as low as 0.6 mg/*l* at these depths. Lasenby [19] found that in late August and early September the mysid population in eutrophic Stony Lake, Ontario, migrates horizontally across the lake to the mouth of a small creek. They remain there for about 6 to 8 weeks. This horizontal migration of the population across the lake coincides with extreme deoxygenation in the deep part of the lake. In September the oxygen concentration at 27 m in Stony Lake was too low to be measured by the standard Winkler technique.

Horizontal migrations may be triggered by low D.O. concentrations or as a response to temperature. In the majority of previous studies, mysids were found in the deepest zones year around, except in the special cases where D.O. became depleted in the hypolimnion. Mysids were not usually found in shallow water during the summer. Tattersall and Tattersall [3] described the general distribution pattern for *Mysis* in accordance with seasons. During the summer *Mysis* migrated to deeper waters and then returned to shallower waters in the winter to breed. Reynolds and Degraeve [29] found that in Lake Michigan the depth distribution of *Mysis* changed noticeably as the season progressed. During the summer and fall *Mysis* concentrated below 55 m, while from January to March adult mysids were collected at depths as shallow as 27 m. Beginning in April the adults moved progressively lakeward. The population during the summer was substantially greater below 73 m than in the shallows. Reynolds and Degraeve suggested a breeding migration of adults to shallow water during the winter, release of the young in these areas in spring, and a consequent return to depth as the water warmed.

Methods and Materials

A traverse line was established from a point near the outlet of the lower lake extending westerly across the lake and ending in the vicinity of the powerplant coffer dam in the northwest corner of the lake. (See fig. 21.) A similar traverse line was established in the upper lake from the connecting channel to the inlet to the upper lake. Each traverse line was divided into equal sections. The lower lake traverse line contained eight sections of approximately 0.4 km in length and the upper lake traverse line contained two sections of 0.8 km in length. During each monthly sampling period, one sample was collected from a randomly chosen length of each section of the traverse lines. In addition, three samples were collected at random from areas less than 15 m deep and three from areas greater than 15 m deep in Lower Twin Lake, along with one sample from an area of depth greater than 15 m in the upper lake [44].

The samples were collected with a large benthic trawl having a mouth width of 1.5 m. The trawl was similar to and operated in the same manner as the trawl described and used in the vertical migration work. The basic procedure consisted of positioning the net on the lake bottom in the selected sampling area. Then 30 to 45 metres of cable were released, depending on the depth, to assure a trawling angle of no more than 30°. Sampling was accomplished at a computed rate of 0.3 to 0.5 m/s for a period of 2 minutes. At the end of the sampling run the trawl was winched vertically to the barge deck. The duration of the haul in seconds multiplied by the computed boat speed in metres per second gave the length of the haul. Each sample was mechanically subsampled and counted, and the count was expanded to represent the total. With the above information, the number of mysids per square metre of lake bottom was estimated.

Two methods of patterned sampling were used to determine how *Mysis* density varied within a small sample area as compared to the entire lake. Six hauls were collected in a grid system in which each trawl originated on a sample transect and crossed two others, resulting in a square-shaped pattern. A radial replicate pattern was also used, consisting of 10 hauls in which each haul resembled a vector with a unique direction beginning at a single center point. Both grid system and radial replicates were taken in the bay in front of the powerplant and in a location near the center of the lower lake (fig. 22). The procedure for collecting, counting, and calculating these samples was identical to that

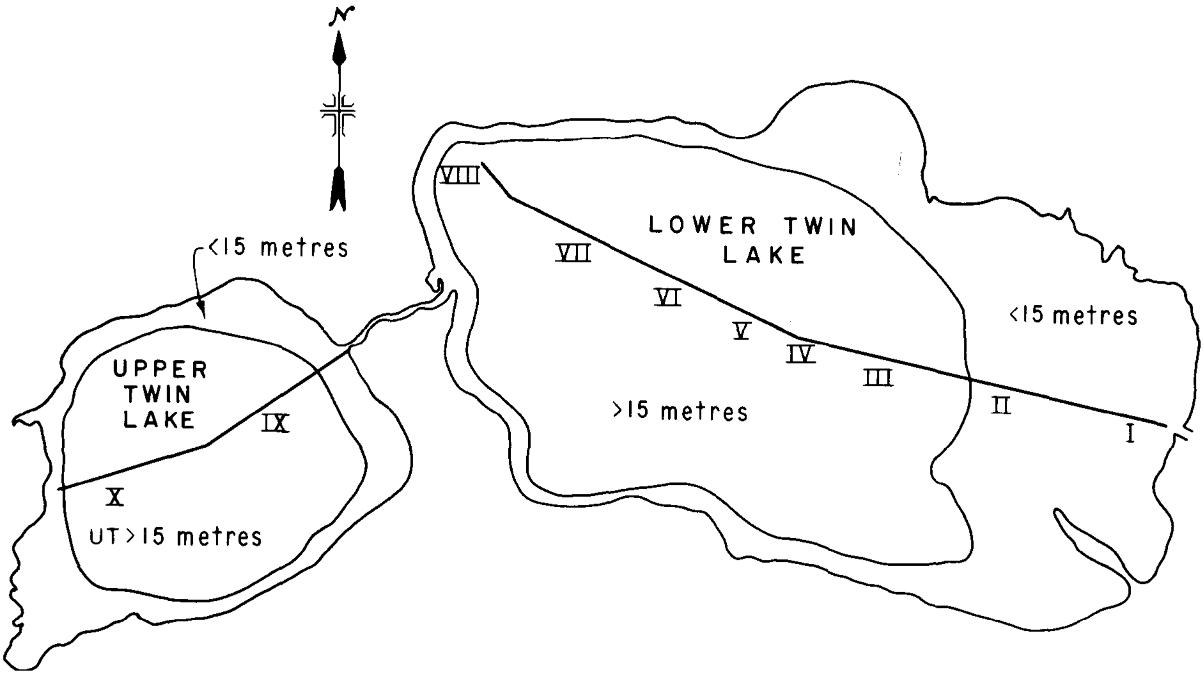

Figure 21.–Location of monthly trawl samples taken in Twin Lakes, Colo. In Lower Twin Lake 3 samples per month were collected at random in areas of < 15 metres and 3 were taken from areas of > 15 metres depth. In the upper lake one sample was collected at random in an area of > 15 metres depth.

used in the regular monthly samples. These samples were collected August 7 to 14, 1975.

Results

The results of 2 years of regular monthly trawl samples are given in table 1. The columns are averaged horizontally to give the mean number of mysids per square metre at each station for samples collected during the 2-year period. The columns are averaged vertically to give the mean number of mysids per square metre for 17 samples collected during each month. Results of the radial and grid replicate sample hauls collected during August 1975 are given in table 2.

Discussion and Conclusions

Dive Reports.—Observations of distribution of *Mysis* in Twin Lakes were made during a series of dives by the Bureau of Reclamation Lower Missouri Regional Dive Team. Dives were made during June 1974, August 1974, and June 1975. Observations were made on the occurrence of *Mysis*, the type of substrate or vegetation present, the approximate density of occurrence, and notable water conditions during the dive [16]. The author made a dive during August 1975 to observe *Mysis*.

Divers consistently observed that mysids are ubiquitous in the Twin Lakes system. Mysids were seen anywhere from a depth of 1.5 metres in bright sunlight to the complete darkness of the lake bottom. They were found in all types of substrate; rocky rubble, sand, glacial flour, and vegetation zones. Very large concentrations of *Mysis* were observed during daylight on a rocky, sandy shelf at a depth of 2.4 metres. Estimates of mysid abundance ranged from 10 to 50 per square metre to a maximum of 500 to 1000 per square metre. Mysid densities were quite variable. During one dive in 3 to 5 metres of water on the southeast corner of the lower lake, between 500 and 1000 *Mysis* per square metre were reported among pondweed (*Pontomageton* sp.) and other vegetation. During the following dive made in the same area at a depth of 1.5 to 3 metres, very few mysids were observed.

Table 1.—*Number of "Mysis" per square metre captured in the benthic trawl in Twin Lakes*

Stations	6/74	7/74	8/74	9/74	10/74	11/74	6/75	7/75	8/75	9/75	10/75	11/75	Ave.
I	N.S.*	7	1	19	8	43	6	62	19	73	32	25	27
II	2	10	14	96	94	57	24	44	23	6	26	15	34
III	5	21	52	96	81	56	6	19	57	33	38	21	40
IV	16	41	98	136	73	N.S.*	6	62	71	81	7	24	56
V	31	39	130	88	37	45	18	8	121	39	9	48	51
VI	33	44	41	101	40	62	28	3	57	39	15	22	40
VII	24	45	3	162	39	86	18	51	67	72	10	15	49
VIII	28	53	65	73	35	80	31	47	81	59	6	6	51
IX	18	44	32	18	45	N.S.*	N.S.*	6	26	23	8	1	22
X	N.S.*	51	31	61	61	N.S.*	N.S.*	7	17	40	29	7	36
1<15	15	14	1	56	63	N.S.*	22	18	12	13	23	13	23
2<15	10	25	4	25	80	17	20	7	37	10	37	18	24
3<15	12	N.S.*	14	66	104	20	17	30	18	N.S.*	24	34	34
1>15	8	10	64	18	24	35	38	18	74	45	36	3	34
2>15	14	46	67	84	31	N.S.*	27	25	35	95	56	14	45
3>15	23	43	111	83	50	N.S.*	35	2	26	56	24	26	49
UT>15	17	29	6	46	14	N.S.*	N.S.*	14	2	19	26	2	17
Ave.	17	33	43	72	52	50	21	25	44	44	24	17	

*No sample.

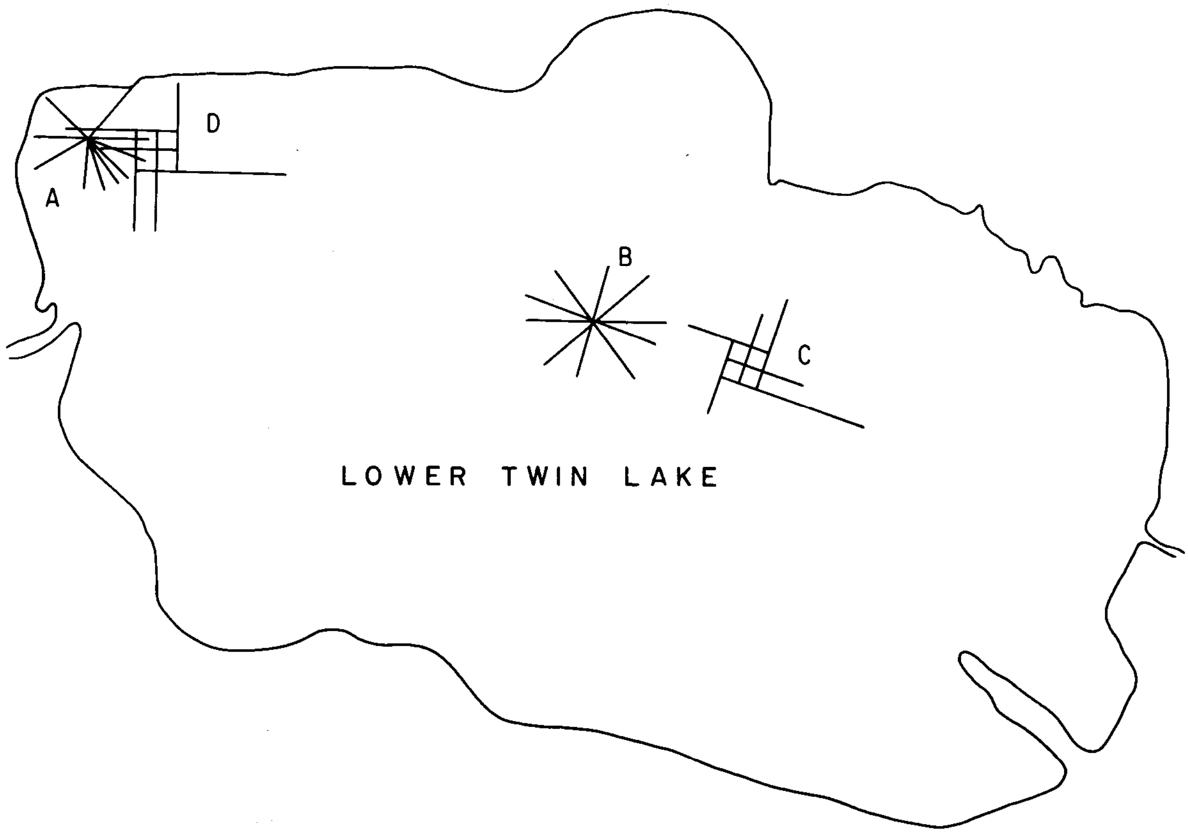

Figure 22.–The location and configuration of patterned samples collected from Lower Twin Lake during August 1975.

Table 2.–*Number of "Mysis" per square metre taken during patterned trawl samples in August 1975 in Lower Twin Lake*

Sample No.	Radial A	Radial B	Grid C	Grid D
1	119	72	59	33
2	116	38	31	96
3	26	31	35	N.S.*
4	21	34	88	118
5	107	127	101	80
6	77	31	79	108
7	127	68		
8	66	79		
9	135	48		
10	98	69		

*No sample.

In all cases where glacial flour substrates were examined, varying number of mysids were also present. On two occasions, groups of *Mysis* sighted in shallow water were composed of mainly immature shrimp. The following section from the June 1975 dive report gives insight into the manner in which the *Mysis* population is distributed:

> The *Mysis* shrimp that were observed occurred in the greatest densities that we had ever seen. The densities ranged up to 300 to

> 400 per square metre with a majority of the shrimp being immature. The pockets of shrimp densities observed last year (1974) ranged from 215 to 270 per square metre. It should be understood that the shrimp occurrences observed on this dive were also pocket occurrences and were not to be interpreted as occurring throughout the entire bottom area [16].

It should be noted that no mysids were seen in the water column during the day. They were always seen within 0.20 m of the bottom. Dives were also made in the outlet stream below the lakes. Deep holes in this stream were examined, but no mysids were found.

Negative binomial distribution of benthic "Mysis".— This analysis sought to determine the distribution pattern of benthic dwelling *Mysis* and to detect spatial and temporal changes in the density of *Mysis*. The spatial dispersion pattern of a population can be an essential factor in understanding the ecology of a benthic invertebrate. Knowledge of the distribution pattern of benthic *Mysis* facilitated both the comparisons between samples and the assessment of environmental factors on density.

The densities of mysids per square metre for 190 samples taken over 2 years were summarized in a frequency distribution. Class intervals contained 5 mm, were nonoverlapping, and began at the size of 1 mm; zero was a separate class. A known mathematical distribution was used as a model for the calculated distribution of samples from the population. The relationship between the sample mean and variance was determined by the actual population dispersion, and the mathematical probability distribution model used is thus dependent on the relationship of mean and variance.

The calculated variance was significantly greater than the calculated mean for the sample. This indicates a contagious or clumped distribution. Several mathematical distributions have been used as models for this situation, and, in particular, the negative binomial has been used as a suitable model for invertebrate populations [45]. Frequent occurrences of contagious distributions have been recorded and there are diverse patterns of contagion. The negative binomial has been used to fit a variety of these contagious patterns. One common pattern is due to patches of high density on a general background of low density.

Elliot [46] gives a formula for fitting the negative binomial to a contagious frequency distribution. His method and the maximum likelihood equation were used to estimate the exponent K of the binomial. The expected frequencies were calculated and the fitted curve is shown along with the actual frequency distribution on figure 23. A "chi-square goodness of fit test" was used to determine that the calculated curve, and thus the model, fits the observed data. Because of the small number of samples (5) in the final 12 categories, it was necessary to take the sum of values in categories greater than 105 in calculating this portion of the chi-square. A summary of the calculations involved in fitting the curve is given in table A-4. The chi-square goodness of fit test showed that the observed frequencies were not significantly different (at the 0.05 level) than the frequencies under the negative binomial model (table A-5). Since the negative binomial model fits the observed frequency distribution, it is apparent that the distribution of *Mysis* in Twin Lakes has a clumped or contagious pattern. This contention is in agreement with observations made during scuba dives.

The density data were transformed so that statistical methods associated with the normal distribution could be used (table A-6). The transformation used was chosen in accordance with the frequency distribution of the original counts. The transformation log $(X + K/2)$ was used, where K is obtained from the maximum likelihood equation for fitting the negative binomial [46]. This transformation was appropriate because it eliminated the dependence of the variance on the mean and it normalized the frequency distribution of the counts (fig. 24). Parametric statistical comparisons could then be used on the transformed data.

Spatial and temporal density variations.— Comparisons of mean densities were made to detect spatial and temporal changes in *Mysis* density and to assess the effects of environmental changes. An initial F-test was used in each comparison to test the null hypothesis that both samples came from the same normally distributed population and that,

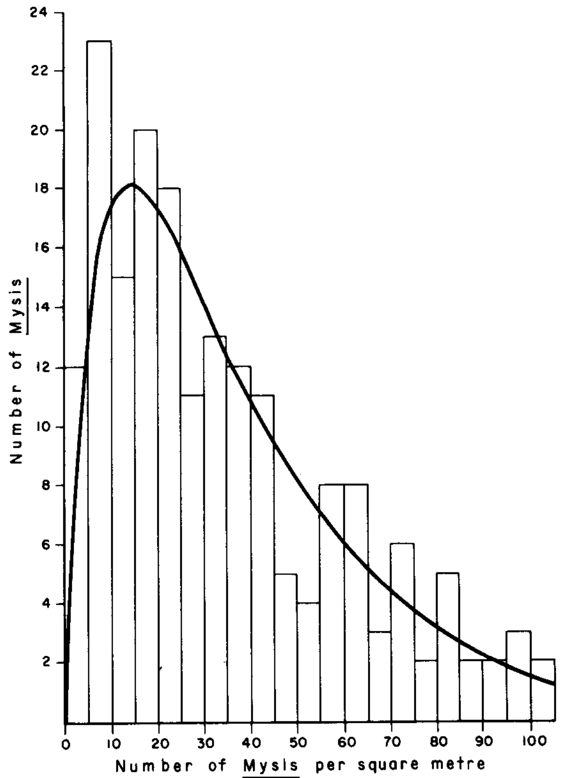

Figure 23.–Histogram giving the actual frequency distribution for 190 samples of *Mysis* per square metre. The solid curve represents a negative binomial frequency distribution fitted to the data.

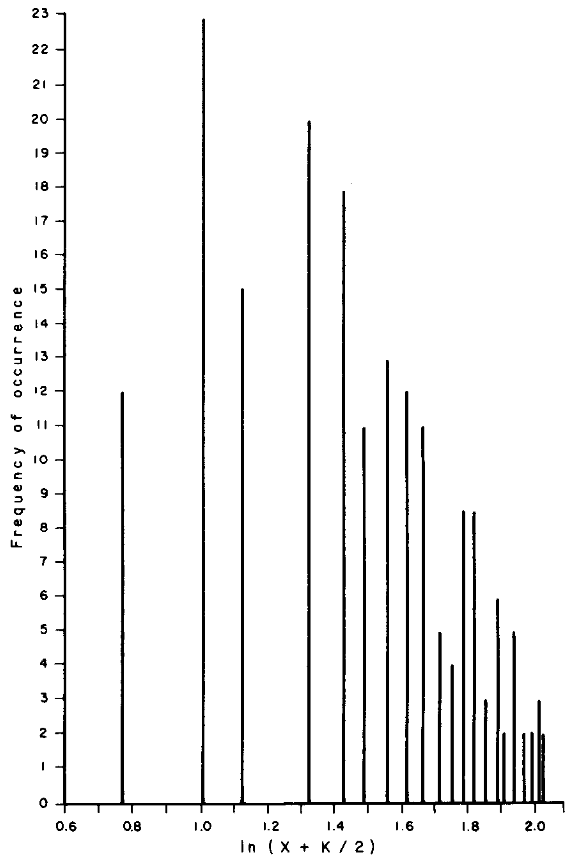

Figure 24.–Frequency distribution for trawl samples after log (X + K/2) transformation. Note that the distribution now approximates the normal distribution.

therefore, there is equality of these estimates of variance. The various samples were then compared using the unpaired t-test to test the null hypothesis that there was no significant difference in the means of samples from the same normal population at a predetermined alpha level, which was taken to be 0.05 in all cases (table A-7).

During summer months Twin Lakes are thermally stratified as shown on the temperature profile graph (fig. 25). Water temperature at depths less than 15 m ranged from 12 to 16 °C, while water temperature at depths greater than 15 m ranged from 7 to 10 °C. Using *Mysis* density data for June, July, and August for 1974 and 1975, a comparison was made between the mean density at five stations of less than 15 m depth versus eight stations of greater than 15 m depth. Comparison of the 28 shallow samples with the 48 deep samples showed a homogeneous variance and a significant difference in mean densities. Mysids apparently prefer deeper, colder water to shallower, warmer water during summer months. Data used in mean density comparisons are given in table A-8.

In the fall, water temperature begins to drop in September, and by October and November the lake is isothermal (see fig. 25). Using data taken during the fall in 1974 and 1975, comparisons were made between the mean density of 28 samples taken at five stations less than 15 m and the mean density of 45 samples taken at eight stations greater than 15 m. The results indicated a homogeneous variance and no significant difference in mean densities. The mysids had changed their distribution from the one favoring deeper, colder water during the summer to one

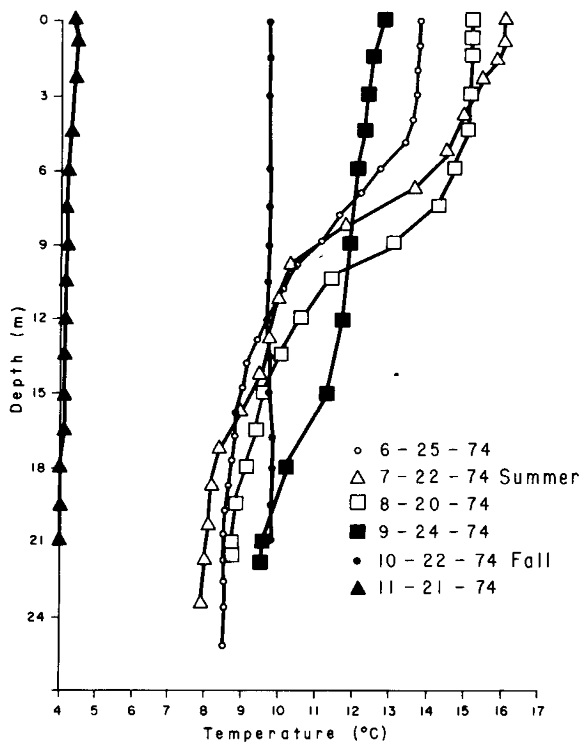

Figure 25.–Seasonal temperature profile in Lower Twin Lake.

of equal distribution between deep and shallow water during the fall. Further F- and t-tests were computed between mean densities in water less than 15 m during summer and fall. Twenty-eight samples from five shallow stations taken during two summers showed a significantly lower mean density than 28 samples taken from the same five shallow stations during the corresponding fall seasons. This result substantiates the indication given by the first two comparisons by showing a definite movement of mysids into shallower water as the water cools in the fall. These findings agree with those of Tattersall [47] and Reynolds and Degraeve [29].

From an inspection of monthly average densities during 1974 and 1975, it was apparent that densities had decreased in 1975. Comparisons between the mean densities for all samples taken in 1974 and mean densities for all samples taken in 1975 indicated a significantly greater mean density during 1974.

Studies on chironomids and copepods have shown the upper lake to have less secondary production than the lower lake [62]. Mean density of *Mysis* for samples from the two lakes were compared and a significantly higher mean density was found to exist in Lower Twin Lake. Samples taken during 2 years at three stations in the upper lake (IX, X, UT) (see fig. 21) were compared with similar samples taken from three stations (II, VIII, 3 > 15) in the lower lake.

The cause of changes in mean density between 1974 and 1975, as well as the mean density difference between the upper and lower lakes, was found during the winter of 1975. Historically, the two lakes had been very similar limnologically [48]. With the advent of transmountain water diversion, the upper lake has become increasingly polluted with heavy metals from mine tailings in the watershed of Upper Lake Creek. The upper lake acts as a settling basin for heavy metals (Fe, Cu, Mn, Zn, and Pb) which become trapped in the upper layers of bottom sediments. During late April and early May 1975, the dissolved oxygen content of the bottom 3 metres of the hypolimnion became depleted. A corresponding change in the oxidation reduction state was recorded. Heavy metals were released into solution from the bottom sediments during the reduction state. An increase of heavy metals to toxic levels in the lake water was recorded in the spring of 1975. During the summer of 1975, chironomids and copepod numbers were found to be greatly reduced in the upper lake [62]. F- and t-tests on transformed data were used to compare the *Mysis* mean densities for all Upper Twin Lake samples from 1974 with those from 1975. The results showed a significantly higher mean density in 1974. Apparently oxygen depletion at the bottom of the winter hypolimnion and associated effects of heavy metals returning to solution were a significant factor in reducing *Mysis* numbers in the upper lake in 1975.

The distribution of benthic *Mysis* within a small area was compared with the distribution of *Mysis* over the entire lake. Grid and radial replicates represented samples taken within a small area in August 1975. The radial replicates consisted of 10 samples taken in the two small areas, while grid replicates consisted of 6 samples taken in two similar small areas (fig. 22). The entire lake sample consisted of the 14 lower lake samples taken during the August 1975 sampling period. All data were recorded as *Mysis* per square metre and transformed by log (X + K/2). Variance comparisons were made using the F-test previously described. The variance of the entire lake sample was compared with radial A, radial B, grid C, and grid D samples. No significant differences in variance were found. This result shows that *Mysis* density in four small areas was not significantly more homogeneous than it was over the entire lake in August 1975. This implies that the clumped distribution of *Mysis* density is apparent even within a small area.

THE IMPACT OF PUMPED STORAGE

Twin Lakes and Mt. Elbert Pumped-Storage Powerplant

The present Twin Lakes Reservoir on Lake Creek has a capacity of 90 000 cubic dekametres. The project plan provides for a new dam downstream from the present structure, creating an enlarged reservoir inundating both lakes and having a capacity of 181 000 dam^3. The new reservoir will receive native flows from Lake Creek, transmountain water presently imported by the established Independence Pass Tunnel, and project water released from Turquoise Lake, which will reach Twin Lakes via the Mt. Elbert Conduit, Mt. Elbert Forebay, and the Mt. Elbert Pumped-Storage Powerplant (fig. 26).

A pumped-storage powerplant such as the Mt. Elbert plant has both generating and pumping cycles. During periods of peak power demand for domestic and industrial needs, water will be released from the forebay to operate turbine-driven generators. During periods of minimum power consumption, water will be pumped to the forebay from Twin Lakes, using excess power from distant fossil fuel powerplants to operate the units as motor-driven pumps. The powerplant is designed for two 100-MW units that can be operated separately. It is planned to begin initial operation with a single unit. The initial contract included construction of one complete 4.6-m-diameter steel penstock approximately 915 metres long and 4.6-m-diameter steel stubs for the second penstock. Each unit will be rated at 123.4 metres of head and 101.66 m^3/s and will have a minimum generating capability of 100 megawatts under all reservoir storage elevations.

The forebay occupies a ridge above Twin Lakes and is contained by a dam at its north end and a dike at the south end. An outlet channel from the southeast corner of the reservoir connects to the inlet-outlet structure for the penstock. The forebay is lined with an impervious layer of silt clay.

Powerload curves show that summer peaks are long and flat as a result of air-conditioning loads, while winter peaks are sharper in nature and shorter, being shaped mainly by lighting loads. The Mt. Elbert plant is capable of operating a maximum of 23 hours per day, with 12 hours for generation and 11 hours for pumping. Peaking power demands are greatest in the summer and may require the maximum capacity available. Power demands decrease in the spring and the fall. Actual plant operation will be dictated by the demands of the power network and may be modified by environmental concerns such as the vertical migrations of *Mysis*.

The recurrent operation of the powerplant for peaking power production and pumping will cause daily water level fluctuations in the lakes and in the forebay. The average fluctuation in Twin Lakes with one unit operating will be 0.23 m when the lake is at its average level. With two units operating, the average fluctuations will be 0.47 m. Maximum predicted fluctuations, short of a power failure, are 0.67 m for Twin Lakes and 4.54 m in the forebay. The most pronounced water level changes resulting from powerplant operations will occur when Twin Lakes and the forebay are near their minimum storage levels.

Twin Lakes will be most frequently near its minimum level when the plant is operating. Maximum possible seasonal flucuation of the reservoir water surface is about 12.19 m; however, in any one year it will fluctuate considerably less, averaging 5.49 m. Maximum fluctuation will be in early summer and the minimum in late summer.

The design of the tailrace channel determines the manner in which water will enter and leave the lower lake. Hydraulic studies conducted by Bureau engineers determined the most feasible model from several possible designs:

> A distorted, thermally stratified, rigid bed model (1:100 vertical, 1:600 horizontal) was

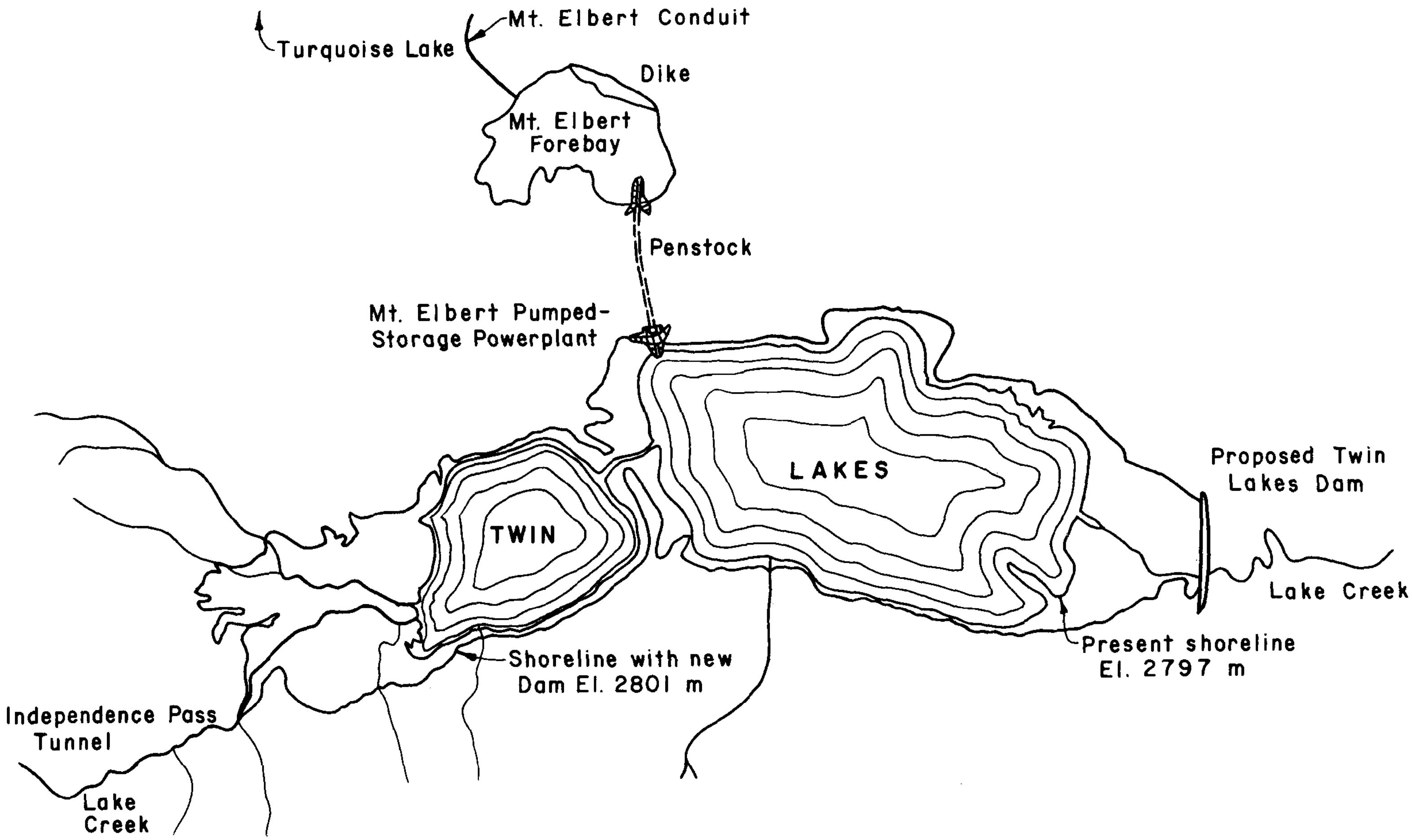

Figure 26.–Map of Twin Lakes and the Mt. Elbert Pumped-Storage Powerplant showing the lakes as they exist at present, the proposed dam, and the new shoreline (adapted from [2, p. II-73]).

used to study destratification effects and circulation patterns in detail. The model included both lakes, the connecting channel, the inflow and outflow channels, and the Mt. Elbert plant. Plant operation was controlled by a minicomputer which also scanned thermistors, applied calibration corrections, and printed temperatures. The thermistors were placed in vertical strings at several locations in the lower lake and at one location in the upper lake. The latter was used primarily to monitor any heat exchange between the model and ambient laboratory air, since the upper lake is unaffected by plant operation. Velocities in the model were measured with an electromagnetic current meter and circulation patterns and jet movement were determined by single frame photography of dye clouds. An undistorted (1:100) homogeneous model was used to examine the near field characteristics of the jet and to develop the design of the tailrace channel. The bed was formed with sand to allow easy modification. Velocities were measured with a miniature propeller meter and an electromagnetic current meter [49].

After considering several models, the channel selected for the prototype installation angled 27° to the right of the pumping-generating plant centerline. The channel has a bottom elevation of 2789 m, an 18-m bottom width, and 3-to-1 side slopes. At the end of the channel where it enters the lake, a berm 1.5 m high and 3.0 m wide serves as an underwater barrier. The barrier is to encourage withdrawing water from a higher level during the pumping cycle and to influence the inflowing jet during the generating cycle so that it will have less tendency to move along the bottom of the lake.

The plant outfall (el 2786 m) is separated from the lakeshore by a channel 274 metres long. The top of the berm at the end of the channel will be at elevation 2790 m. The shoreline is currently at elevation 2797 m; with the new dam it will be approximately 2801 m. There is a 45° slope from the shoreline to the bottom of pump plant bay, which is fairly uniform in depth, ranging from 2777 to 2779 m in elevation. Since water levels can fluctuate a maximum of 12 m, with a fluctuation of 5.8 m in any one year, the depth of the channel will be quite variable. The channel inlet will be 12 m above the bottom of pump plant bay and 16.8 m above the minimum lake bed elevation of 2774 m. Upon completion of the new dam and with the new maximum water surface at 2805 m, the channel inlet will be 15 m undeı the surface. These features will be important when considering the impact on the *Mysis* population. (See fig. 27.)

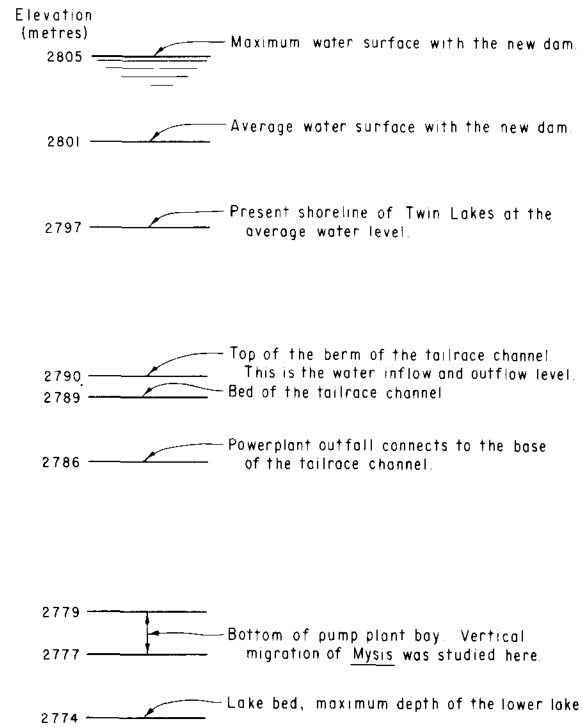

Figure 27.–The relationship between water surface elevations, tailrace channel elevations, and the bottom elevation of Lower Twin Lake.

Velocity distribution measurements were made in studies using the undistorted model. Tests simulated two units operating at maximum discharge: 172.7 m^3/s for the pumping cycle and 203.9 m^3/s for the generating cycle. Separate tests made with the lake surface at 2797 m and at 2801 m indicated that during the pumping cycle most of the water entered the channel from along the north shore of the lake. The flow was evenly distributed and velocity was about 0.37 m/s. Water movement along the west shore was not appreciable. As water moved into the plant, a large circling motion was created directly in front of the channel inlet. The average velocities in this area were close to 0.15 m/s, with slightly greater velocities at the surface than at depth. Water movements were alike at both water surface levels. Water in the channel moved more rapidly as it neared the powerplant intake. At 2797-m surface elevation, water velocity in the channel averaged 0.58 m/s at all depths. The 2801-m surface elevation had an average inflow velocity of 0.28 m/s over all depths. Thus, the higher water level significantly decreases the velocity of water flowing into the plant (see fig. 28).

Tests to determine the flow data during the generating cycle showed that the jet leaving the plant stayed close to the west shore, then turned eastward when it reached the south shore of the lower lake. During the generating cycle, flow was not evenly distributed near the plant; but it did attain an adequate distribution by the time it entered the lake, where average velocities were less than 0.30 m/s. Velocities were slightly higher from middepth down. Figure 29 shows flow data with two units generating at 203.9 m³/s.

The effect of the inflow during power generation on thermal stratification was tested in the modeling studies. In the area immediately adjacent to the tailrace, the thermal stratification pattern was rapidly upset. This proved to be a localized effect. The stratification pattern for the entire lake was not affected by two-unit

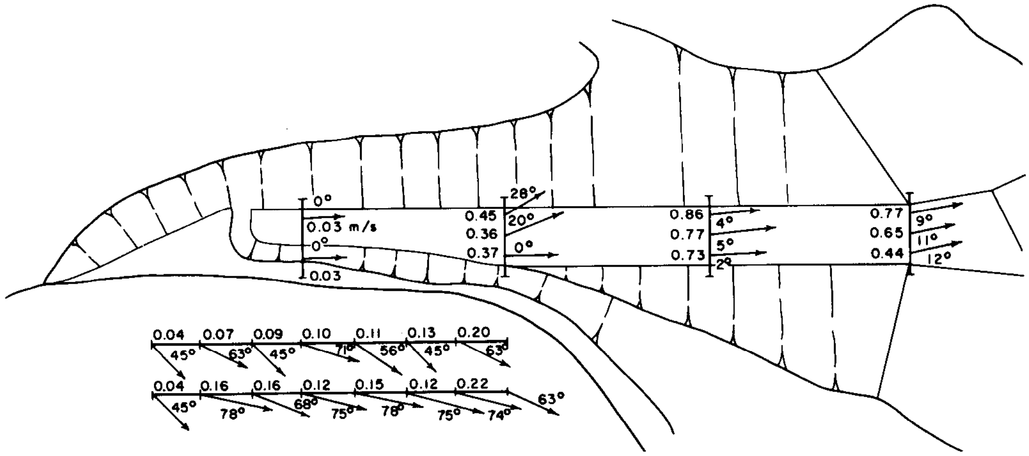

Figure 28.–Velocity distribution measurements made during Bureau of Reclamation model studies on the powerplant tailrace channel. Arrows indicate the direction of water flow and velocities are given in metres per second. This indicates the water flow at the 9-metre depth with two units pumping 172.7 m³/s with the lake at water surface elevation 2797 metres (data from [49]).

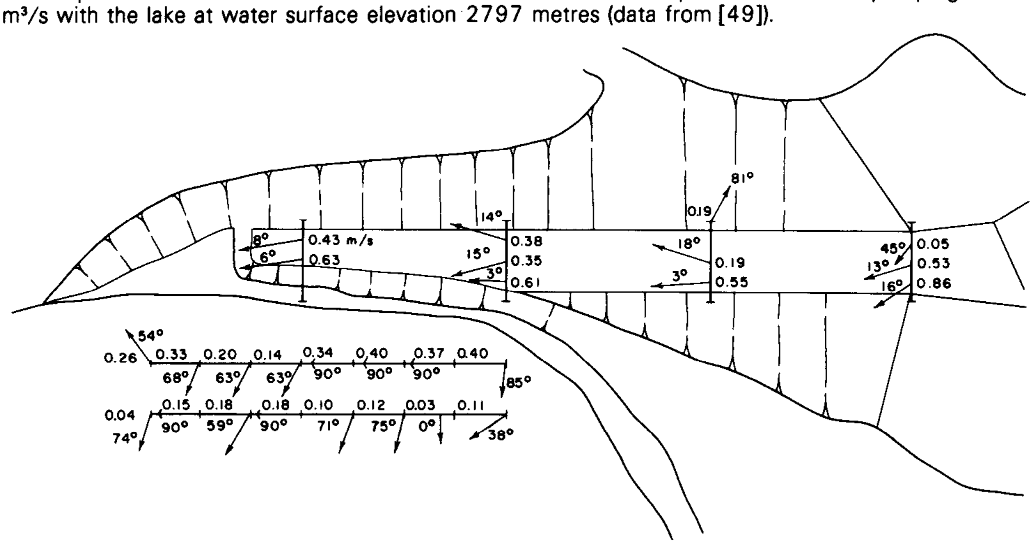

Figure 29.–Velocity distribution measurements made during Bureau of Reclamation model studies on the powerplant tailrace channel. Arrows indicate the direction of water flow and water velocities are given in metres per second. This indicates the water flow near the bottom with two units generating at 207.9 m³/s. The lake surface elevation was 2801 metres during this test (data from [49]).

operation, although there was a tendency for the ambient temperature to be affected by the temperature of the generating flow. Over a 2-week operating period, cold-water inflow lowered the lake temperature and warm-water inflow increased the temperature, while the gradient remained essentially the same. Nineteen days of simulated operation did not affect the temperature of the upper lake [49].

To test the effects of the inflow jet during generation on the glacial flour sediments, dye tracers were placed in the lake bottom of the model in the vicinity of the glacial flour sediments. During the initial 2 or 3 days of operation, the dye tracers did not move and they were gradually assimilated into the surrounding water. Dependent on temperature conditions, the situation where the forebay contains colder, and thus denser, water than that in the lake could cause a diving jet which could disturb the bottom sediments.

The large amounts of water necessary to operate the pumped-storage plant must be considered. During the pumping cycle with two units operating, 172.7 m^3/s will be lifted to the 13 600 dam^3 forebay. The excess water needed for 203.9 m^3/s generation will come to the forebay via the Mt. Elbert Conduit. The combined volume of Twin Lakes at present is 90 000 dam^3. Assuming a 9-hour pumping period with two units pumping 172.7 m^3/s, this would mean that 6.2 percent of the volume of Twin Lakes passes through the turbines during this cycle. With the new dam and corresponding maximum volume of 181 000 m^3, a 9-hour pumping cycle would account for 3.1 percent of the total volume of the lakes.

Possible Impacts on "Mysis"

To obtain information on the possible impact of pumped storage on *Mysis*, a series of laboratory experiments was conducted. Predicting long-term effects of pumped storage on a population is difficult, but it was possible to determine short-term effects of specific factors on *Mysis* survival. Conditions in the lake may be altered by the plant operation in three ways: (1) turbulence will be created in the powerplant area and the forebay, (2) turbidity from the resuspension of glacial flour sediments may result, and (3) thermal stratification in the lake may be altered.

Model studies showed that both pumping and generating cause turbulence in the northwest corner of the lake. Entrained *Mysis* would be subjected to extreme turbulence in passing through the plant and the penstocks. In the forebay, *Mysis* would be subjected to continued turbulence. The possibility of a mysid in the forebay becoming entrained a second time would be high. The ability of *Mysis* to survive turbulence, whether it be from entrainment or from living in the area adjacent to the plant or in the forebay, was investigated. *Mysis relicta* have never been reported to live in flowing waters. Mysids are not normally subjected to currents and because this animal is fragile, the possibility exists that it may become physically exhausted or suffer mechanical abrasion from turbulence.

The possible resuspension of glacial sediments by the inflow jet poses a serious problem. McNatt [50] measured 1 to 2 kilograms of suspended solids per acre-foot of water transported via a pumped-storage plant into Canyon Lake, Ariz. During the construction of the cofferdam and the road in front of the Mt. Elbert plant, the lower lake became turbid and many days passed before the sediments settled out. Model studies with dye tracers showed that the present tailrace design prevented the glacial flour from being moved. If the glacial flour were resuspended, such as by a diving jet of cold water from the forebay, it would be virtually impossible for the flour to settle out because of daily generating and pumping. Therefore, it would be valuable to know how turbidity would affect *Mysis*.

The model studies determined that the upset of thermal stratification would be localized in the immediate area adjacent to the tailrace. Over the entire Twin Lakes system, the models showed a very slight temperature alteration with no change in the basic patterns. It is therefore unlikely that the predicted temperature change will have any significant effect on *Mysis*.

"Mysis" in Laboratory Aquaria

Mysis were held in the laboratory for use in tolerance tests and for general observation. Environmental conditions are quite specific for *Mysis* and several methods of holding them in the laboratory were used before adequate survival was maintained.

Mysis collected at Twin Lakes were transported to the laboratory in coolers filled with lake water and ice. Because laboratory water supplies were too warm for *Mysis*, fiberglass Min-O-Cool troughs and cooling units were used to lower the water temperature to 5 to 8 °C. Aquaria of varying sizes were partially immersed in the troughs to hold the mysids. The troughs thus acted as a water bath to maintain aquarium temperatures. A very slow inflow of water was maintained in each aquarium. Aeration was not provided, but *Mysis* survival was good without it. The fluorescent laboratory lamps were connected to a timing device which delivered 8 hours of light and 16 hours of darkness. The lamps were partially screened with cardboard and thus light was diminished during the day period. Having the aquaria inside the dark fiberglass troughs further reduced the light reaching the mysids.

Different types of substrate including gravel, Twin Lakes sediments, and bare glass, did not adversely affect *Mysis* survival. *Mysis* were fed a mixture of finely ground tropical fish food, trout food, and a vitamin complex used by fish hobbyists. *Mysis* were observed to move rapidly about in the cloud of food when they encountered it. They did not actively come toward the food, but passively wandered into it and then, upon perceiving the food, they moved rapidly about in a seemingly random manner.

Mysis generally spend most of their time resting their appendages lightly on the substrate. They do not burrow, but the constant motion of the pereipods creates a swirling current which can pick up small particles and detritus from the substrate. They make random forays into the water column and occasionally swim inverted along the surface, pulling in small particles. Observations were made of mysids carrying a fragment of plant material or part of a dead *Mysis*. On the bottom of the aquaria *Mysis* had a tendency to rest in groups. The majority of the mysids would be grouped in one area and the remainder of the tank would have very few individuals.

In August 1974, *Mysis* were put in laboratory aquaria and held for 1 year. They were checked periodically for growth and sexual development. The development of sexual characteristics followed the life cycle exhibited in Twin Lakes. Young-of-the-year mysids were less than 10 mm in length and, as was expected, they remained immature during the winter of their first year. During the fall, adult male and female mysids developed sexual characteristics. In January, adult males were completely mature with the fourth pleopod extending well beyond the telson. Approximately half the females were brooding at this time. During February and March, the majority of adult females were carrying broods. At this time adult males died off at sizes of less than 17 mm. Development of the broods failed in all cases. Adult females with partially developed broods died in some cases and in others the brood pouch remained empty. In May and June, the only mysids in the aquaria were 1-year-old immatures and a few large adult females (up to 21 mm) with empty brood pouches. Conditions in the aquaria apparently were not conducive to *Mysis* reproduction.

Effects of Turbulence and Turbidity on "Mysis" Mortality

Twin Lakes *Mysis* that had been acclimated to laboratory aquaria for several months were subjected to turbulence and turbidity in varying degrees to determine the increase in mortality over a period of 8 days. The trials were conducted as a factorial experiment using three levels of turbidity (0, 735 to 779, 1470 to 1558 APHA turbidity units [64]) and four levels of turbulence ($K = 0$, 1.9, 3.0, 5.2). Twelve cells were used, each having one unique combination of the two factors. The cell having zero turbulence and zero turbidity served as a control for each trial. The turbulence was created by individual diaphragm aerators. Aerator operation was controlled by a timing mechanism. The turbulence began at 2400 hours, continued for 8 hours, and then shut off at 0800 hours. After a 16-hour rest period, the cycle was repeated. The sediments causing turbidity began to settle out during the rest period and were resuspended during the turbulent period. The greater the turbulence the more thoroughly the sediments remained in suspension.

Each trial began with 20 *Mysis* per cell. The cells were 7-litre, 150-mm-diameter plastic cylinders. The cylinders stood upright in a fiberglass Min-O-Cool trough maintained at a constant temperature of 6 °C. Each cylinder was equipped with a drain at the bottom and a removable screen matching the inside diameter of the tube. At a designated time on the second, fourth, sixth, and eighth days, *Mysis* in each cell were examined to determine the degree of mortality that had occurred. During a counting period, each cylinder was removed from the water bath and drained into a holding bucket. The mysids were retained on the screen for easy transfer to a sorting tray where the number of dead and living *Mysis* was determined. A mysid was considered dead when no movement could be observed. Following the count, the screen was replaced in the cylinder and the original water; and the surviving mysids were recorded and replaced. Mysids were fed every other day. Laboratory lighting was reduced as previously described.

The turbidity was created with sediments collected from pump plant bay. Portions of these sediments were put into suspension by stirring with a magnetic device for a period of 6 hours. After allowing 1 hour for the sediments to settle, supernatant was siphoned off without disturbing the heavier sediments which had settled out. The supernate contained a high concentration of very fine particles which remain in suspension. This concentrated solution was used as the high turbidity level. The middle level was produced by diluting the concentrated solution one-to-one with well water. The zero turbidity level was pure well water.

Turbidity was measured with the Hellige turbidity meter. Dilutions of the original sample were made to the measurable range. The volume of turbidity-free water used for dilution divided by the volume of the sample gave the dilution factor. The product of the dilution factor and the measured turbidity gives the original turbidity.

To conduct this experiment it was necessary to create a measurable turbulence in the experimental cylinder containing *Mysis*. Turbulence infers total water movement. Measuring turbulence would necessitate determining alternating surges and microcurrents in conjunction with orderly streamlined flow. Current meters and mechanical measuring devices would be impractical in this situation. Because this experiment sought to determine the effects on *Mysis* and not to expend large amounts of time or resources seeking to measure turbulence, it was most practical to select a measuring device that was readily available and adaptable to determining turbulence in experimental containers.

The reoxygenation or diffusion constant, K, is directly proportional to the total water movement or turbulence in a system. If air is released in a container of water, the result is the creation of turbulence in proportion to the amount of air released. If K is proportional to turbulence and turbulence is proportional to airflow, then a relationship can be established between K and airflow. This theory was incorporated into this experiment by using varying rates of airflow to create different levels of turbulence, and by measuring the turbulence in terms of K by determining the relationship between airflow rate and the reoxygenation constant, K. In this experiment then, K was used as a relative measure of turbulence.

The reoxygenation constant, K, is the negative instantaneous rate at which water becomes reoxygenated. The rate at which a cylinder of water with low oxygen concentration becomes reoxygenated can be calculated using an adaptation of the universal formula for a negative instantaneous rate. This is computed by knowing the initial concentration of oxygen, the final concentration of oxygen, and the time interval elapsed between measurements [51].

$$K = \frac{\log_e Ctx - \log_e Cto}{tx}$$

where

Ctx = final concentration expressed as mg/ℓ below saturation
Cto = starting concentration expressed as mg/ℓ below saturation
tx = experiment duration in hours.

By varying the amount of air released into a cylinder of deoxygenated water and calculating the K in each case, a correlation between air release in cm^3/min and K was established.

Deoxygenated water was obtained by vigorously boiling water in a large metal pot. This was added to the cylinders that had been tempered to prevent expansion cracks. Melted paraffin was poured across the mouth of the cylinders to seal them. Cylinders were then cooled in the water bath to experimental temperatures of 6 °C. Air was supplied to each cylinder using separate diaphragm aquarium aerators. Stopcock-type valves, PVC tubing, and glass tubing completed the air delivery system. The bare end of the glass tubing served to regulate the release of air bubbles. Air was released at the center of the cylinder.

Airflow rates were calibrated using a funnel-top buret inverted over the air stream. A stopwatch recorded the time required for the airflow to replace a known volume of water in the buret column. Airflow rates were adjusted to desired levels in surrogate cylinders before the determination of K values.

The paraffin covering on the test cylinders was removed and a water sample was taken. The Azide modification of the Winkler method was used for dissolved oxygen determinations. The aeration tubes were then inserted in the jars for a measured time. At the end of the time period the aeration tubes were removed and a final D.O. measurement was made.

Four rates of airflow were used to establish the correlation with K (see table A-9). The relationship is shown to be linear in figure 30. In the factorial experiment, the turbulence was created using airflow rates of 340, 680, and 1360 cm^3/min. Using the equation of the line given in figure 30, the K values corresponding to these airflow rates were calculated as 1.9, 3.0, and 5.2, respectively (see table A-10).

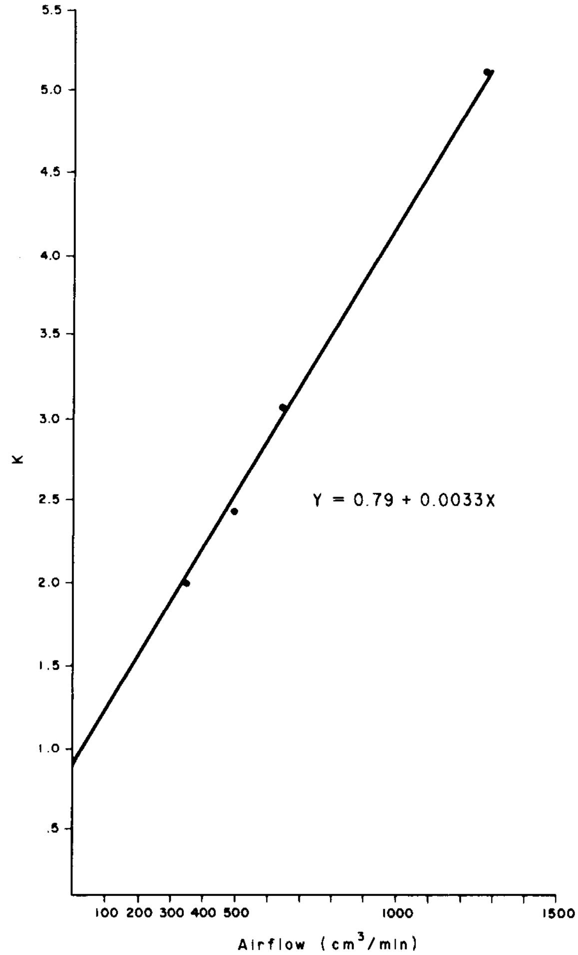

Figure 30.–The relationship between airflow rate in cm^3/min and the reoxygenation constant, K, as it was determined from four experimental cylinders.

Experimental Design and Analysis

The experiment was designed to fit a "factorial analysis of variance" format. The factors in the analysis included: (1) turbidity at three levels (0, 735 to 779, 1470 to 1558 APHA turbidity units [64]); (2) turbulence at four levels (K = 0, 1.9, 3.0, 5.2); (3) trial replicates numbered 1 to 4; and (4) time of counts in days after beginning the trial (2, 4, 6, and 8 days).

The data were first investigated as a regular four-way analysis of variance (table A-11); they were then regrouped into a split-plot design which was used to group between-cell variation due to main factor and to replicate effects separately from within-cell variation due to repeated measure of the time factor. Winer [52, p. 337] gives the method of analysis of a factorial experiment where the last factor has repeated measure. The between-cell variation was made up of the first three factors. Turbulence and turbidity and the interaction between these two factors make up most of the main-effect variation. The replications are included essentially as a third factor in this analysis. Part of the between-cell variation is due to replication effects as well as interactions with replications. In a replicated design of this type, interactions with replications are considered to be part of the experimental error [52, p. 215]. After regrouping the analysis to the split-plot design with the last factor having repeated measure, the analysis of variance is that shown in table 4.

Results and Discussion

Each trial consisted of 12 cylinders subjected to one of the combinations of turbulence and turbidity. Each experimental cylinder was assigned to a specific combination of treatments and was used for the same combination of treatments in each of the four trials. The number of *Mysis* alive at each count out of the original 20 per cylinder are shown as individual entries in table 3.

Turbidity showed no significant effect on mortality, but turbulence significantly increased mortality. Linear regression between turbulence, K, and main-effect mean mortalities due to turbulence gave a highly significant correlation coefficient of 0.998. The interaction of turbidity and turbulence did not appear to significantly influence mortality. Examination of the two-way means verifies this (table A-12). An interesting effect was noted in that the lowest level of turbulence caused greater mortalities as turbidity decreased. This was noted during the experiment and was quite obvious in the two-way means. At the lowest level of turbulence, the higher turbidities actually improved *Mysis* survival.

The replicate factor gave a significant F value due to variation between trials. The trial variation shows the variation in mortality between separate groups of *Mysis*. One factor which could account for this variation is temperature. In both the first and third replicates, the temperature was above the desired 6 °C; in these cases temperature was slightly above 9 °C. *Mysis* mortality caused by turbulence and by experimental handling seems to be increased by temperature stress. Interactions between factors 1 and 2 and replications were incorporated into error term A.

The within-cylinder variations in mortality were attributed to the time factor. A highly significant F shows that the longer *Mysis* were exposed to factors 1 and 2, the greater the resulting mortality. Linear regression between time and mortality gave a highly significant correlation coefficient of 0.998. There was some interaction between time and turbidity, which was judged to be due to the large main effects of time, but this interaction was not considered important. A similar situation was evident between time and turbulence, where the interaction was significant, but largely the result of the large main effects of the separate factors. This interaction was examined graphically to determine its expression. The graph in figure 31 shows an increase in the slope of the mortality

Table 3.—*Results of the turbulence and turbidity trials on "Mysis" mortality (Table entries indicate the number of "Mysis" alive at each count out of the original 20)*

Turbidity[1]		0					735-779					1470-1558				
Turbulence[2]		0	1.9	3.0	5.2	Total	0	1.9	3.0	5.2	Total	0	1.9	3.0	5.2	Total
Days	Trials															
2nd	1	17	8	9	12	46	19	7	0	0	26	18	18	11	3	50
	2	20	19	19	10	68	20	18	17	9	64	20	20	17	9	66
	3	17	17	13	12	59	20	16	11	5	52	19	19	15	0	53
	4	19	18	15	10	62	20	20	18	6	64	20	19	18	4	61
	total	73	62	56	44	235	79	61	46	20	206	77	76	61	16	230
4th	1	15	7	8	7	37	17	5	0	0	22	16	16	6	1	39
	2	19	18	16	6	59	20	12	12	3	47	20	20	14	4	58
	3	15	12	10	7	44	19	10	4	5	38	18	15	11	0	44
	4	19	14	12	6	51	19	17	14	3	53	20	17	10	3	50
	total	68	51	46	26	191	75	44	30	11	160	74	68	41	8	191
6th	1	15	3	2	0	20	16	2	0	0	18	15	11	5	0	31
	2	18	13	13	4	48	19	9	2	2	38	19	17	10	4	50
	3	13	6	8	0	27	17	9	0	0	29	17	13	9	0	39
	4	18	8	7	2	35	18	17	6	1	42	20	14	6	1	41
	total	64	30	30	6	130	70	37	17	3	127	71	55	30	5	161
8th	1	14	0	2	0	16	15	1	0	0	16	15	11	3	0	29
	2	14	10	10	0	34	17	4	6	1	28	17	16	6	0	39
	3	11	0	0	0	11	14	7	0	0	21	16	11	8	0	35
	4	18	1	0	0	19	18	17	0	0	35	20	11	2	0	33
	total	57	11	12	0	80	64	29	6	1	100	68	49	19	0	136

[1] American Public Health Association turbidity units.
[2] Reoxygenation constant, K.

Table 4.—*Analysis of variance using the four-factor split-plot design with repeated measure to determine the effect of turbulence and turbidity on "Mysis" mortality (The fourth factor time had repeated measure. Trials were included in the between-cell variation)*

Source	Degrees of freedom	Sum of squares	Mean square	F value	Significance at alpha = 0.05
Between Cell Variation					
Turbidity	2	126.03	63.02	3.30	NO
Turbulence	3	3,438.81	1,812.94	94.99	YES, highly
Turbidity X Turbulence	6	399.43	66.57	3.49	NO
Trials	3	750.40	250.13	13.11	YES
Error A	33	629.80	19.08		
Within Cell Variation					
Time	3	1,476.73	492.24	152.08	YES, highly
Time X Turbidity	6	89.01	14.84	4.58	YES
Time X Turbulence	9	209.76	23.31	7.20	YES
Time X Turbidity X Turbulence	18	69.77	3.87	1.20	NO
Error B	108	349.56	3.24		

line with time only as the turbulence goes from zero to the first K value of 1.9. After this, the slopes of the mortality lines at K of 3.0 and 5.2 were not significantly affected. This shows that any interaction between time and turbulence had only minor importance. The three-way interaction between time, turbulence, and turbidity was not significant. Interactions between time and the replicate factor were included in error B.

Conclusions

Turbidity had no effect on *Mysis* mortality in laboratory cylinders; however, turbulence caused a linear increase in *Mysis* mortality as K increased. There was no significant interaction between these two factors. The four replicates of the experiment showed significant variability which can be attributed to natural differences between groups of *Mysis*. Experimental observations indicated that an increase in temperature from 6 to 9 °C caused increased mortality among *Mysis* subjected to turbidity and turbulence. Mortality also showed a linear increase across time in the 8-day experiment. Interactions between turbidity or turbulence and time had only minor effects on *Mysis* mortality.

"Mysis" Reaction to Turbulence

Mysis are not usually associated with turbulent flow and it was shown in the previous experiment that mortality increased when they were exposed to turbulence for 8 hours daily. The response of *Mysis* to turbulence in pump plant bay will partially determine what effect plant operation will have on them. The question of whether they will move into or out of the area or remain where they are was considered. *Mysis* have shown the ability to vacate an area when conditions are unsuitable. Migrations due to low D.O. concentration [19] and changing temperatures [29] have been recorded. If *Mysis* developed an avoidance reaction to the turbulent area, then the possibility of entrainment would be decreased. The opposite possibility also exists. They may have a tendency to congregate in the inflow-outflow area. This would increase the possibility of entrainment and

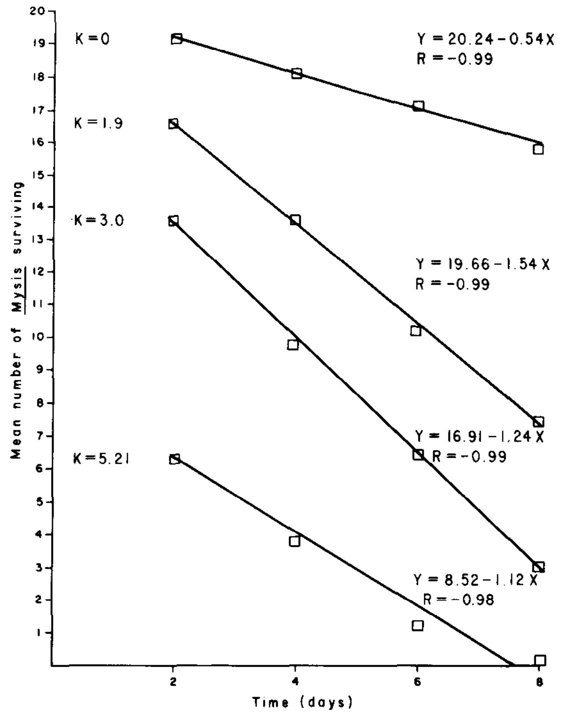

Figure 31.–The interaction between turbulence and time is examined by plotting mean numbers of *Mysis* surviving at each level of turbulence versus time. Mean number of *Mysis* surviving was obtained from the two-way means with the time factor on the horizontal and the turbulence factor on the vertical (table A-12).

thus would increase mortality and have a greater adverse effect on the mysid population.

A simple laboratory experiment was undertaken to determine mysid reaction to turbulence. A fiberglass Min-O-Cool trough was equipped with a cooling system as previously described. The cooling unit was partitioned off at one end, and a slow flow of water from the cooling unit to a screened standpipe drain at the opposite end maintained trough temperature at 6 °C. The trough was marked lengthwise into quarter sections. An aeration device or a submersible pump was placed in the end section to create a turbulence. No attempt was made to measure turbulence quantitatively. With no turbulence in the trough, a number of *Mysis* (25 to 100) from the aquarium stock were equally distributed along the length of the trough. The mysids were allowed 48 hours to acclimate and distribute themselves in the trough. Counts were then made of the number in each quarter section. This was used as the control and was repeated three times.

The turbulence was then started: in trials 1 to 5, the aeration device was used to create turbulence; and in trials 6 to 10, a submersible pump was used. In each case *Mysis* were left in the trough for 48 hours and then the number in each quarter section were counted. Quarter sections are designated as cells in the analysis.

The results of individual replicates are numbered and presented graphically in figures 32 and 33 for turbulence trials and figure 34 for control trials. The turbulence was created in cell No. 4 during the trials.

The control and trial replicates were considered separately. The sum of the *Mysis* occurring in each cell for three controls and for 10 trials was computed. A chi-square goodness of fit test was used to test the hypothesis that mysids were equally distributed among each quarter of the trough. One-fourth of the total number of mysids was expected in each cell of the trough (see tables A-13 and A-14).

The chi-square test gave a nonsignificant value (4.62) for the controls and a highly significant value (410.64) for the turbulence trials (table chi-square = 7.81, 3 d. f. (degrees of freedom), $\alpha = 0.05$). The hypothesis of equal distribution was accepted for the control. Figure 34 shows the relatively equal distribution between the four cells. The hypothesis of equal distribution was rejected for the turbulence trials. The graphs of each replicate in figures 32 and 33 show a consistent pattern of *Mysis* avoidance to cell 4 where the turbulence was located. Regardless of the source of turbulence, the number of *Mysis* increased with increasing distance from the turbulence.

CONCLUSIONS

Mysis relicta will be entrained in the Mt. Elbert plant. The area adjacent to the tailrace channel contained an average density of 36 *Mysis* per square metre. These mysids have been shown to undertake diel vertical migrations of varying intensities. At the present water surface elevation, the bed of the tailrace will be at a depth of 7.6 m and the top of the berm at 6.1 m. The percentage of the population occupying this portion of the water column during the hours from 2200 to 0600 hours averaged 17.6 percent of the population in the area. The

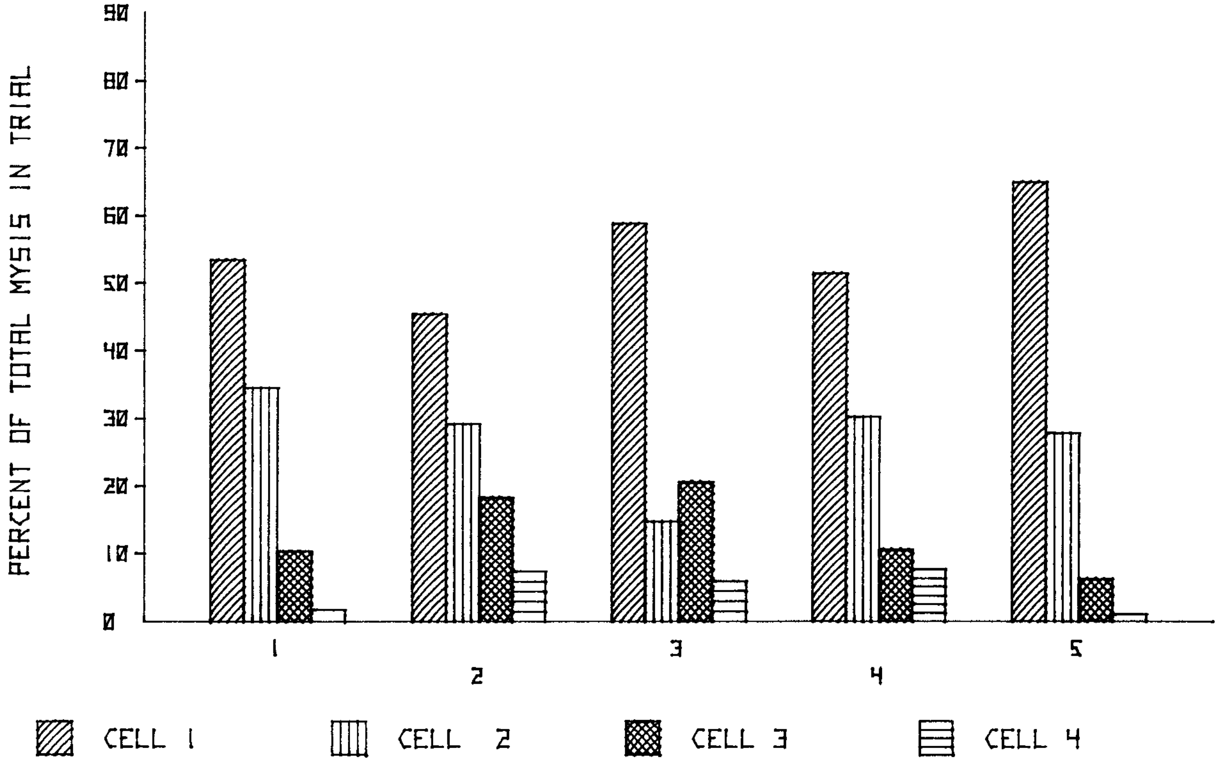

Figure 32.–Turbulence trials. Each cell represents one quarter section of the trough. The turbulence was created in cell 4. Each histogram shows the percentage of the total number of *Mysis* that were located in each cell after 48 hours with turbulence created by an aeration device.

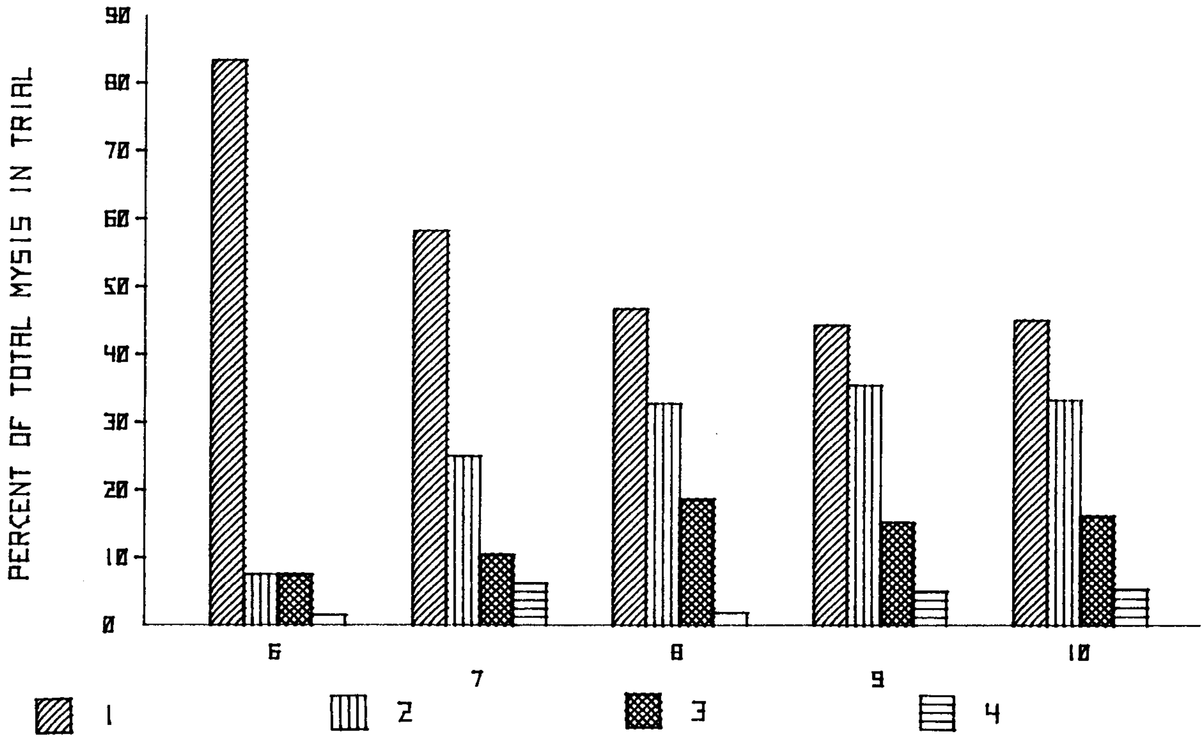

Figure 33.–Turbulence trials. Each cell represents one quarter section of the trough. The turbulence was created in cell 4. Each histogram shows the percentage of the total number of *Mysis* that were located in each cell after 48 hours with turbulence created by a submerged pump.

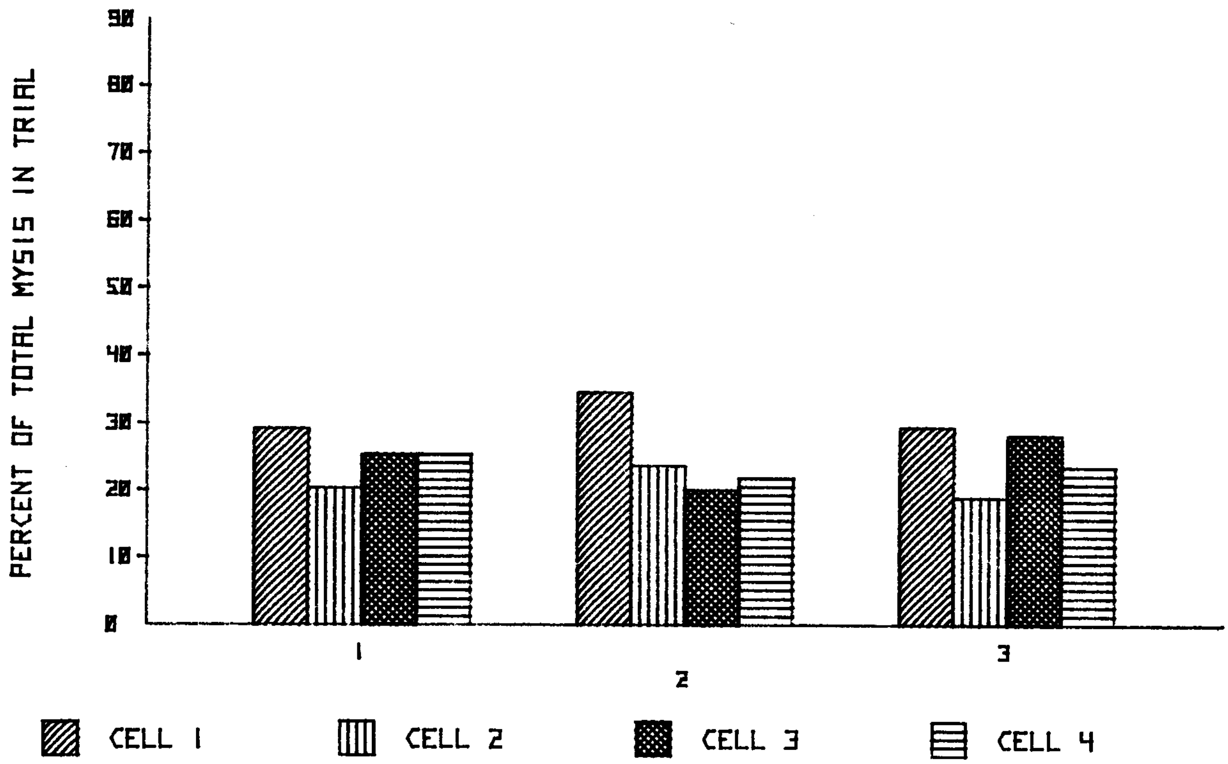

Figure 34.–Control trials. Each cell represents one quarter section of the trough. Turbulence was turned off during control trials. Each histogram shows the percentage of the total number of *Mysis* that were located in each cell after 48 hours.

percentage ranged from 1 to 56 percent. The hours from 2200 to 0600 hours will then be the most critical to the entrainment of *Mysis.*

Water velocities greater than 0.15 m/s flowing into the tailrace during the pumping cycle are sufficient to carry *Mysis* into the tailrace. Mysids occupying the depths from 9 m to the surface from 2200 to 0600 hours will be subject to velocities of this magnitude. Mysid densities in this area vary according to seasonal temperature patterns and light intensities. During the summer when the lake is thermally stratified, numbers of *Mysis* congregate below the thermocline. At this time they will be particularly vulnerable to entrainment. Juveniles occur in the shallow waters with greater frequency than adults and therefore the juveniles will be entrained in greater numbers.

The tendency for *Mysis* to move into the shallows in the fall and winter when the lake becomes isothermal may also increase the possibility of entrainment. The inflow water moves mainly along the north shoreline and mysids in this area would likely be carried along with the flow. During a 9-hour pump-back cycle where 6.2 percent of the water of Twin Lakes is taken into the plant, it is likely that substantial numbers of *Mysis* will be entrained.

Entrainment of fish eggs and larvae, as well as zooplankton, by powerplants has been documented in several studies. Topping and Ratzlaff [53] found that 100 to 250 million zooplankton per day passed from Muddy Run Reservoir to Conowingo Reservoir through the Muddy Run Pumped-Storage Plant. Robbins *et al.* [54] concluded that phytoplankton, zooplankton, and larval stages of benthic insects are regularly pumped into Muddy Run Reservoir. They also concluded that any fishes present below the pumped-storage plant soon became established in the upper reservoir. Carlson and McCann[55] predicted that large numbers of eggs, larvae, and young-of-the-year striped bass would be withdrawn from the Hudson River estuary by pumping at a proposed hydroelectric pumped-storage plant at Cornwall. Liston and Tack [56] documented that a variety of fish species found in the adjacent area of Lake Michigan were subject to entrainment in the Ludington Pumped-Storage Powerplant. Forage fish species in the area near the powerplant showed a decline during 2 years of plant operation, while zooplankton in the area were not adversely affected. Changes in the populations of forage fish and zooplankton in the Ludington plant area were difficult to attribute to a specific cause due to natural variation occurring in a system as large as Lake Michigan [56, 57]. *Mysis relicta* have been found in the plant outfall at the forebay of the Ludington Pumped-Storage Plant.[4]

Mysis entrained in the Mt. Elbert plant will be subjected to pressure change and mechanical abrasion from turbulence. Marcy [58] in an overview of entrainment of organisms at powerplants, makes the point that mechanical damage can be a major cause of entrainment mortalities. Copepods entering the cooling water system of the Millstone Point Plant at Niantic, Conn., suffered 70 percent mortality due to mechanical and hydraulic stresses of the passage [34]. Beck and Miller [59] determined that mechanical damage from pumps caused 40 percent mortality of entrained phytoplankton and zooplankton. Larger size zooplankton showed an increased mortality over small zooplankton [60]. Mysids apparently are not susceptible to pressure changes in powerplants. In the laboratory, Beck *et al.* [61] studied the exposure of organisms to hydrostatic pressure regimes calculated for the proposed Cornwall Pumped-Storage Plant. *Neomysis americana* showed no significant differences in viability from their control groups when subjected to negative pressure of 2 lb/in^2a followed by exposure to 466 lb/in^2g during pumping, continued through generating, and then back to 2 lb/in^2a.

The turbulence and turbidity tests have shown that *Mysis relicta* suffered substantial mortality when exposed to turbulence. Entrained *Mysis* will undoubtedly suffer some mortality. This mortality will result from a combination of mechanical abrasion, turbulence, and exhaustion of *Mysis* adjacent to the tailrace and in the forebay. A large and fragile zooplankter like *Mysis* will be particularly susceptible to mechanical damage. Turbulence in areas adjacent to the tailrace and in the forebay may last as long as 23 hours in a single day, with 11 hours of pumping and 12 hours of generating.

The possibility of a glacial flour turbidity problem resulting from plant operation does not seem to be critical to the survival of *Mysis*. Turbidity had no detectable effects on the short-term survival of mysids.

The avoidance reaction of *Mysis* to turbulence will have a tendency to keep them away from critical areas. During and immediately following generation, the area adjacent to the tailrace will likely have a decreased density of mysids because of avoidance, which in turn should cause a decrease in entrainment in the subsequent pumping cycle.

Substantial numbers of *Mysis* will be entrained in the Mt. Elbert plant and a significant number of these will not survive. Following initial high localized mortalities, the population in pump plant bay will probably remain diminished; however, seasonal movements will bring some mysids into the area, resulting in continued mortality due to plant operation. The regeneration time for *Mysis* is 2 years, therefore mysid losses caused by the plant will be replaced much slower than they would be for most other species of zooplankton. Whether regeneration of *Mysis* will exceed attrition caused by plant operation is not known.

[4] See footnote 2, p. 1.

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APPENDIX

Table A-1.—*Flowmeter calibration (Kahl digital pigmy flowmeter)*

Distance, H		Volume	Litres	Revolutions	Litres per
feet	inches	in^3			revolution
50	600	3185.4	52.2	56	0.932
50	600	3185.4	52.2	55	.949
50	600	3185.4	52.2	57	.916
50	600	3185.4	52.2	60	.870
100	1,200	6402.7	104.4	118	.885
100	1,200	6402.7	104.4	112	.932
100	1,200	6402.7	104.4	109	.958
100	1,200	6402.7	104.4	119	.877
150	1,800	9556.2	156.6	165	.949
150	1,800	9556.2	156.6	172	.910
150	1,800	9556.2	156.6	165	.949
150	1,800	9556.2	156.6	171	.916

Volume = $\pi R^2 H$
Volume = 3.1416 · 1.3 in^2 · distance in inches = 5.309H
Litres = cubic inches · 0.01639 litres/in^3
Average volume in litres per revolution = 0.920

Table A-2.—*Monthly size frequency totals for all "Mysis" captured during each monthly sampling period*

Size, mm	Months								
	9/74	10/74	11/74	1/75	2/75	4/75	6/75	7/75	8/75
3i									
4i						317	2,544	14	2
5i							9,524	697	1,320
6i							3,404	2,071	4,166
7i	64	0	0	0			782	3,219	7,261
8i	3,878	232	0	0		4	0	1,204	2,575
9i	11,173	2,088	160	0	1	12	0	287	721
10i	1,216	835	708	2	3	9	15	8	75
IM	3,952	3,264	1,020	3	12	20	25	6	59
IF	4,966	2,857	1,106	3	5	10	35	5	60
11IM	4,238	2,510	2,328	5	68	35	36	10	78
IF	2,489	3,232	1,488	6	34	20	26	13	40
12IM	870	375	190	7	35	94	577	74	50
IF	1,063	351	299	11	52	90	693	45	117
MM	2,351	621	40	7	10	0	0	0	0
MF	842	129	0	0	0	7	0	0	0
12IM	0	0	0	0	10	40	1,796	385	799
IF	0	0	0	0	19	55	435	141	412
MM	1,461	1,281	868	13	12	0	0	0	0
MF	1,436	1,681	508	5	24	9	0	0	0
14IM	0	0	0	0	0	0	2,966	783	1,725
IF	0	0	0	0	0	21	1,409	389	609
MM	848	980	569	6	11	0	0	0	0
MF	983	1,306	1,196	5	43	67	588	116	125
15IM	0	0	0	0	0	0	1,592	695	1,072
IF	0	0	0	0	0	0	1,437	348	591
MM	2,797	874	432	4	6	0	0	0	0
MF	1,626	456	656	8	26	28	993	575	524
16IM	0	0	0	0	0	0	260	259	294
IF	0	0	0	0	0	0	326	112	85
MM	1,369	321	173	2	3	0	0	0	9
MF	1,875	541	353	8	6	14	1,066	581	876
17IM	0	0	0	0	0	0	0	28	24
IF	0	0	0	0	0	0	0	8	16
MM	192	77	8	0	0	0	491	0	0
MF	1,344	373	321	3	14	5	536	376	286
18IF	0	0	0	0	0	0	151	0	0
MF	1,436	404	88	0	2	0	950	188	244
19MF	197	17	32	0	0	0	765	98	72
20MF	64	72	0	0	0	0	447	28	50

i = Immature.
IM = Immature male.
IF = Immature female.
MM = Mature male.
MF = Mature female.

Table A-3.—*Average monthly length of "Mysis" cohorts*

Month	Size, mm	
	Juveniles	
4/26	4.00	
6/7	5.15	
7/9	6.77	
8/16	6.84	
9/28	8.83	
	Immature males	Immature females
10/26	10.53	10.61
11/25	10.76	10.72
1/15	11.36	11.40
2/12	11.34	11.77
4/26	11.81	12.29
6/7	13.86	14.43
7/9	14.32	14.55
	Mature males	Mature females
9/28	13.99	–
10/26	13.81	14.57
11/25	13.93	14.74
1/15	13.41	14.97
2/12	13.52	14.56
4/26	–	*14.37
6/7	–	16.82
7/9	–	16.18
8/16	–	16.23

*Small sample.

Table A-4.—*Fitting the negative binomial* $(q - p)^{-K}$ *where:* $p = u/K$, $q = 1 + p$, *u is the arithmetic mean, and K is the exponent*[46]

Calculate:- $\bar{X}, s^2, K$

$$\bar{X} = 36.76$$

$$s^2 = 878.77$$

estimate K, $$K = \frac{\bar{X}^2}{s^2 - \bar{X}} = 1.605$$

The maximum likelihood equation was used to calculate K exactly:

$$n \log_e \left(1 + \frac{\bar{X}}{K}\right) = \Sigma \left(\frac{A(x)}{K + x}\right)$$

$$\Sigma \left(\frac{A(x)}{K + X}\right) = \frac{A(x = 0)}{K} + \frac{A(x = 1)}{K + 1} + \frac{A(x = 2)}{K + 2} \cdots + \frac{A(x = \eta)}{K + \eta}$$

Use K values bracketing the estimated value. Values of 1.2 and 1.6 were used. Solve the above equation using the above values. The differences between the two sides of the maximum likelihood equation are used to solve for K by proportion:

	difference	
K = 1.2	−19.05	$\frac{K - 1.2}{1.6 - 1.2} = K = 1.5472$
K = 1.6	2.92	

Individual probabilities were calculated as follows:

$$P(x) = \left(1 + \frac{\bar{X}}{K}\right)^{-K} \frac{K + X - 1}{X! (K - 1)} \left(\frac{\bar{X}}{\bar{X} + K}\right)^{X}$$

The probabilities were multiplied by the total sample number (η) to obtain the expected frequencies.

Table A-5.—*Chi-square goodness of fit for the negative binomial distribution*

Class interval	Observed	Calculated	Chi-square value
0	0	1.325	1.33
1-5	12	13.243	0.11
6-10	23	17.478	1.74
11-15	15	18.180	0.55
16-20	20	17.594	0.32
21-25	18	16.287	0.17
26-30	11	14.624	0.89
31-35	13	12.664	0.01
46-40	12	11.116	0.07
41-43	11	9.663	0.18
56-50	5	8.341	1.33
51-55	4	7.161	1.38
56-60	8	6.116	0.58
51-65	8	5.197	1.51
66-70	3	4.404	0.44
71-75	6	3.726	1.38
76-80	2	3.141	0.41
81-85	5	2.635	2.12
86-90	2	2.215	0.02
91-95	2	1.854	0.01
96-100	3	1.587	1.25
101-105	2	1.324	0.34
106-162	5	5.552	0.05
			Total 16.19

Calculated chi-square statistics 16.19.
Table chi-square 20 degrees of freedom = 31.41.
There is a significant fit to the negative binomial distribution.

Table A-6.—*Monthly trawl data following the log (X + K/2) transformation*

Stations	Months											
	6/74	7/74	8/74	9/74	10/74	11/74	6/75	7/75	8/75	9/75	10/75	11/75
I	N.S.*	0.891	0.249	1.296	0.943	1.641	0.831	1.799	1.296	1.868	1.516	1.411
II	0.443	1.032	1.170	1.986	1.977	1.762	1.394	1.651	1.376	0.831	1.428	1.198
III	0.761	1.33[illegible]	1.732	1.986	1.913	1.754	0.831	1.296	1.762	1.529	1.588	1.338
IV	1.225	1.621	1.995	2.136	1.868	N.S.*	0.831	1.792	1.856	1.913	0.891	1.394
V	1.502	1.600	2.117	1.948	1.577	1.661	1.274	0.943	2.086	1.600	0.990	1.688
VI	1.529	1.651	1.621	2.008	1.610	1.798	1.459	0.577	1.762	1.600	1.198	1.357
VII	1.394	1.661	0.577	2.212	1.600	1.938	1.274	1.714	1.831	1.862	1.032	1.198
VIII	1.459	1.731	1.818	1.868	1.554	1.907	1.502	1.679	1.912	1.776	0.831	0.831
IX	1.274	1.651	1.516	1.274	1.661	N.S.*	N.S.*	0.831	1.428	1.376	0.943	0.249
X	N.S.*	1.714	1.502	1.791	1.791	N.S.*	N.S.*	0.891	1.250	1.610	1.474	0.891
1 15	1.198	1.170	0.249	1.754	1.805	N.S.*	1.357	1.274	1.106	1.139	1.376	1.139
2 15	1.032	1.411	0.679	1.411	1.907	1.250	1.318	0.891	1.577	1.032	1.577	1.274
3 15	1.106	N.S.*	1.170	1.825	2.020	1.318	1.250	1.488	1.275	N.S.*	1.394	1.541
1 15	0.943	1.032	1.811	1.274	1.394	1.554	1.589	1.274	1.874	1.661	1.565	0.577
2 15	1.170	1.670	1.831	1.928	1.502	N.S.*	1.444	1.411	1.554	1.981	1.754	1.169
3 15	1.376	1.691	2.048	1.923	1.706	N.S.*	1.554	0.443	1.428	1.754	1.394	1.415
UT 15	1.250	1.474	0.831	1.670	1.170	N.S.*	N.S.*	1.170	0.443	1.296	1.428	0.443

*No sample.

Table A-7.—*Formula used in making comparisons of mean densities of "Mysis" from trawl data*

Equality of variance was tested with the F-test.

$$F = \frac{\text{variance 1}}{\text{variance 2}} \qquad \frac{\text{df}_1}{\text{df}_2} = \frac{\text{df}_1}{\text{df}_2} = \frac{\eta_1 - 1}{\eta_2 - 1}$$

Equality of means was tested with the t-test.

$$s^2 = \frac{[\Sigma(y_1^2) - \overline{y}_1\ \Sigma y_1] + [\Sigma(y_2^2) - \overline{y}_2\ \Sigma y_2]}{\eta_1 + \eta_2 - 2}$$

$$t = \frac{\overline{y}_1 - \overline{y}_2}{s\sqrt{\frac{1}{\eta_1} + \frac{1}{\eta_2}}} \qquad \text{d.f.} = \eta_1 + \eta_2 - 2$$

Table A-8.—*Comparisons of mean densities of "Mysis" per square metre in the classification listed below as described in the text. (The data were obtained from the stations listed on the dates listed and the parameters calculated for use in the F- and t-tests are shown. Original data are from the text, table 1.)*

Classification	Stations	Dates	η_1	y	s^2
Summer shallow	I II 1<15 2<15 3<15	6/74 7/74 8/74 6/75 7/75 8/75	28	1.1314	0.1440
Summer deep	IV V VI VII VIII 1>15 2>15 3>15	6/74 7/74 8/74 6/75 7/75 8/75	48	1.5027	.1504
Fall shallow	I II 1<15 2<15 3<15	9/74 10/74 11/74 9/75 10/75 11/75	28	1.4863	.1094
Fall deep	IV V VI VII VIII 1>15 2>15 3>15	9/74 10/74 11/74 9/75 10/75 11/75	45	1.5643	.1375
1974	all stations	6/74 7/74 8/74 9/74 10/74 11/74	92	1.5084	.1733
1975	all stations	6/75 7/75 8/75 9/75 10/75 11/75	98	1.3384	.1445
Upper lake	IX X UT>15	all dates	29	1.2513	.1705
Lower lake	II VIII 3>15	all dates	35	1.4813	.1757
Upper lake 74	IX X UT>15	6/74 7/74 8/74 9/74 10/74 11/74	14	1.4690	.0771
Upper lake 75	IX X UT>15	6/75 7/75 8/75 9/75 10/75 11/75	15	1.0480	.1778

Table A-9.—*Data for determining experimentally the correlation between airflow rate and K*

cm^3/min	Beginning D.O. concentration mg/l	Final D.O. concentration mg/l	Time interval hours	Calculated K
1,275	3.41	9.69	0.5	4.909
648	3.49	9.92	1.0	2.938
485	3.61	9.63	1.0	2.329
340	3.49	9.88	1.5	1.887

Note: temperature was 6^{o} C, altitude was 1500 metres (5000 ft), O_2 saturation was 10.28.

Table A-10.—*Calculated K values resulting from several assumed airflow rates (using the equation $y = 0.79 + 0.0032x$)*

Airflow cm^3/min	Calculated K value
1,360	5.195
680	2.993
340	1.892

Table A-11.—*Factorial analysis of variance used in determining the effect of turbidity and turbulence on "Mysis" mortality*

Source*	Degrees of freedom	Sum of squares	Mean square
Total	191	9,539.20	
1	2	126.03	63.02
2	3	5,438.81	1,812.94
12	6	399.43	66.57
3	3	750.39	250.13
13	6	125.84	20.97
23	9	235.26	26.14
123	18	268.70	14.93
4	3	1,476.73	492.29
14	6	89.01	14.84
24	9	209.76	23.31
124	18	69.70	3.87
34	9	48.34	5.37
134	18	51.61	2.86
234	27	121.93	4.52
1,234	54	127.68	2.36

*1 = turbidity, 2 = turbulence, 3 = trials, 4 = time.

Table A-12.—*Main effect means and two-way means for the factorial analysis of variance used in determining the effect of turbidity and turbulence on "Mysis" mortality*

Main effect means				
Turbidity levels (1-3):	9.94	9.27	11.22	
Turbulence levels (1-4):	17.50	11.94	8.20	2.92
Trials (1-4):	7.29	12.48	9.42	11.38
Time (1-4):	13.98	11.29	8.71	6.58

Two-way means

Turbidity	Turbulence			
	1	2	3	4
1	16.38	9.63	9.00	4.75
2	18.00	10.69	6.19	2.19
3	18.13	15.50	9.44	1.81

Turbidity	Trials			
	1	2	3	4
1	7.44	13.06	8.81	10.44
2	5.13	11.06	8.75	12.12
3	9.31	11.31	10.69	11.56

Turbidity	Time			
	1	2	3	4
1	14.69	11.94	8.12	3.00
2	12.86	10.00	7.94	6.25
3	14.37	11.94	10.06	8.50

Turbulence	Trials			
	1	2	3	4
1	16.00	18.58	16.33	19.08
2	7.42	14.67	11.25	14.42
3	3.83	12.33	7.67	9.00
4	1.92	4.33	2.42	3.00

Trials	Time			
	1	2	3	4
1	10.17	8.17	5.75	5.08
2	16.50	13.67	11.33	8.42
3	13.67	10.50	7.91	5.58
4	15.58	12.83	9.83	7.25

Table A-13.—*Distribution of "Mysis" in a trough without turbulence (used as the control distribution)*

Replicate number	Cell 1	Cell 2	Cell 3	Cell 4	Total
1	23	16	20	20	79
2	19	13	11	12	55
3	25	16	24	20	85
Total	67	45	55	52	219

Chi-square goodness of fit		Ho: Equal distribution in all cells	
Expected frequency	54.75	Chi-square	4.62
OBS-EXP^2/EXP Cell 1	2.74	Degrees of freedom	3.00
OBS-EXP^2/EXP Cell 2	1.73	5% crit. value	7.81
OBS-EXP^2/EXP Cell 3	0.001	Not significant	
OBS-EXP^2/EXP Cell 4	0.13	Do not reject Ho	

Table A-14.—*The distribution of "Mysis" in a trough with turbulence*

Replicate number	Cell 1	Cell 2	Cell 3	Cell 4	Total
1	31	20	6	1	58
2	25	16	10	4	55
3	20	5	7	2	34
4	34	20	7	5	66
5	63	27	6	1	97
6	55	5	5	1	66
7	28	12	5	3	48
8	50	35	20	2	107
9	35	28	12	4	79
10	42	31	15	5	93
Total	383	199	93	28	703

Chi-square goodness of fit		Ho: Equal distribution in all cells	
Expected frequency	175.75	Chi-square	410.64
OBS-EXP^2/EXP Cell 1	243.88	Degrees of freedom	3.00
OBS-EXP^2/EXP Cell 2	3.07	5% crit. value	7.81
OBS-EXP^2/EXP Cell 3	38.96	Highly significant	
OBS-EXP^2/EXP Cell 4	124.21	Reject Ho	

GPO 842-435

ABSTRACT

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DESCRIPTORS—/ *limnology/ aquatic animals/ lakes/ reservoirs/ powerplants/ *pumped storage/ *environmental effects/ migration/ ecology/ aquatic environment/ benthos/ fish food organisms/ zooplankton
IDENTIFIERS—/ Fryingpan-Arkansas Project, Colo./ Mt. Elbert Pumped-Storage Powerplant, Colo.

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